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Distribution patterns of moss conservation value with implications for conservation management: A case study of Waterton Lakes National Park

by

Jennifer Christine Doubt

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Distribution patterns of moss conservation value: A case study of Waterton Lakes National Park, Canada, with implications for conservation management" submitted by Jennifer Christine Doubt in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

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September 25, 2001

For Waterton Lakes National Park

Abstract

Informed management of a park's floristic resources depends on the evaluation of

a) The establishment of conservation priorities by placing the conservation value of the local flora in the context of the natural regions and political jurisdictions in which it occurs, and

b) The direction of management activities according to conservation priorities by identifying patterns of conservation value within the park.

This task is particularly challenging with respect to taxonomically difficult yet ecologically critical species such as bryophytes, necessitating the development of innovative approaches to facilitating the evaluation of the park and sites within it. In this study, the moss flora of Waterton Lakes National Park, Alberta, Canada is documented, its conservation value (diversity and rarity) is assessed, and the distribution conservation value with respect to spatial and environmental cues is explored. Results provide valuable platform on which to base management decisions for uninventoried land in Waterton, and a flexible template for floristic evaluations of other regions.

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1. INTRODUCTION

1.1 Mountain plant diversity and rarity

Since the first explorations of mountain plant ecology were documented in 1554 (Körner 1999), the world's mountains have held a certain fascination for plant ecologists. In that mountainous regions are infamous reservoirs of endemism and rarity (Körner 1995, 1999) occurring at almost all latitudes (Körner 1999), they are ecologically distinct. However, they share at least two unifying ecological characteristics:

1) **The world's steepest terrestrial environmental gradients, on both micro and meso scales, occur in mountains.** There is no such thing as 'alpine climate' (Körner 1999; Tivy 1993) but mountains are characterized by remarkable climate variability (Körner 1995). Large altitudinal variation produces a range of temperature conditions that are consistently compared to change in temperature with latitude (Körner 1999; Tivy 1993) – on a much smaller geographic scale. With increasing elevation, the environment generally becomes more inhospitable to plant growth. Temperatures, for example, fall, atmospheric pressure decreases (reducing the partial pressure of carbon dioxide and increasing evaporation), maximum radiation and short wave radiation rise, and mechanical disturbance increases (Körner 1999; Tivy 1993). Precipitation falls increasingly as snow.

   Fine-scale climate variation is also of unparalleled magnitude and importance. Even within the broadly harsh high-altitude habitat matrix there are embedded thermal microgradients of dramatically different character (particularly in sunshine). Alpine plants selected (evolutionarily) for their small size rely increasingly on avoiding the hostile environment by occupying atypical microhabitats. Körner (1995, 1999) reports that the climate of alpine plants depends largely on solar radiation, topography (slope and exposure), and plant stature, as well as the modifying influences of wind velocity (affecting heat loss, evaporative cooling, and precipitation patterns), ambient temperature, and the structure and thermal conductivity of the substrate. Elevation becomes less valuable as a predictor of plant life conditions with increasing altitude (Körner 1995, 1999).

2) **Mountainous habitats feature high plant diversity compared with surrounding lowlands.** Although plant diversity generally decreases with increasing altitude (e.g. Körner 1995, 1999;

Pastor 1995), the geographical compression of ecological gradients leads to an overall diversity that is extremely high. Plant communities change progressively in character from basal plains to mountain tops. Vegetation forms distinct zones reflecting altitudinal climate change (e.g. Daubenmire 1943; Tivy 1993), and fine-scale climate variation enriches each community. The geographic and climatic isolation of mountains along with the migrational and evolutionary histories of plants also account for high plant diversity in mountains (Körner 1995, 1999). Tivy (1993) reports that mountains feature the highest plant diversity of any terrestrial habitat, citing in part the preponderance of relict and endemic species, the richness of growth conditions, and the presence of unique habitats.

Many environmental constraints shaping plant ecology in mountains have also limited human activity (Tivy 1993). In highly populated countries, some of the only remaining wilderness reserves occur in mountain habitats (Körner 1999). Their relatively pristine character and abundance of habitats makes them practical and exciting settings for ecological discovery and conservation. Blessed as they are with compelling scenic magnificence, however, mountain parks worldwide draw increasing numbers of visitors, so that the preservation of their natural character is no longer assured. This pressure lends a sense of urgency both to ecological research (including the documentation of ecological resources) in mountains and to the development and application of judicious, scientifically-based protective measures.

1.2 Factors shaping the northern Rocky Mountain flora

Quaternary (Pleistocene) glaciation by Laurentide and Cordilleran glaciers eliminated most vegetation from the northern Rocky Mountains (e.g. North 1976), although the existence of an ice-free corridor has long been discussed (e.g. Moss 1955; Rutter 1980). Initial recolonization by plants took place from the southwest, southeast, and east, with migration from the east, west and north becoming possible much later as the continent warmed (North 1976). Whereas boreal floristic elements are thought to have survived glaciation in the Appalachians and the Bering Straits area, Cordilleran species occupied refugia in the south-west (North 1976). These plant groups mix along the east slopes of the Rockies, where the Cordilleran and Laurentide ice sheets met. The mountains of the north-temperate and boreal regions of North America were floristically linked during the cold phases of the quaternary period, so they have not

experienced the prolonged isolation characteristic of southern mountains (Tivy 1993). The Rockies also maintain a physical link to the arctic, and provide a migrational corridor far into the south.

Glaciation in the Rockies not only dictated the suite of colonizing species, but also contributed the physical characters that form a key part of plant habitats. Valleys were made deeper and slopes, steeper (North 1976). An enormous variety of substrate textures, slopes, and elevations was left behind, leading to a richness of growth conditions and of plants unsurpassed in the region. Fire and erosion, affected in large part by slope and aspect, continue to shape patterns of vegetation throughout the Rockies.

1.3 Plant ecology in Waterton Lakes National Park, Alberta, Canada

Waterton Lakes National Park, established in 1895, is Canada's southernmost Rocky Mountain park. It forms a small (540 km^2), northern component of Waterton-Glacier International Peace Park, which straddles the 49th parallel and the continental divide. Elevation in Waterton ranges from 1280 to 2940m. Most rock is limestone. Situated on a major pacific storm track, Waterton-Glacier features a maritime climate relative to Rocky Mountain regions to the north and south, even east of the continental divide. The flora and vegetation, as a result, better reflect patterns in Idaho and Washington (Kuchar 1973), than the continental standard set in the rest of Canada's Rocky Mountain parks. Waterton reports some of the highest precipitation totals in Alberta (Kuijt 1982) in mesic forests near the continental divide, and encompasses a transition to semi-arid grassland. The wide local range of habitats and the presence of maritime habitats allows many plants and animals to extend their ranges into the Park, which is well-known for exceptional biological diversity. As Waterton marks the southern-most point in Alberta's Rockies it is also well situated to host temperate floristic elements with ranges centred in the United States. Ecological richness is also derived from glacial history: the Geological Survey of Canada (in North 1976) indicates that Waterton was among the first Alberta regions to be exposed by deglaciation, 15 000 to 17 500 years before present.

Botanical exploration in Waterton Lakes National Park has been reviewed by Kuchar (1973), who has also described the Park's habitat types in detail. As well-known as the unique, rich flora of Waterton is, the park has received little recent botanical attention. The first plant list was published in 1957 (Breitung), and a complete vascular flora was published by Kuijt (1982). Current reports suggest that the

area supports more than 970 vascular plant species (Parks Canada 2000). Non-vascular plants were first investigated by Bird in the late 1960s (1968a,b, 1969a,b), and Hermann (1969) produced a list for Glacier National Park that included several Waterton records. An ecological land classification for Waterton (Achuff et al. 1997) is currently in production.

1.4 Plant conservation challenges and goals in Waterton Lakes National Park

Most conservation activities are concentrated in parks and protected areas, which, as previously noted, are often set in mountainous regions. Most parks are small in size (Stohlgren et al. 1997), and operate on shrinking budgets. Increasing industrial and resource development drives recreational traffic into parks and threatens the ecological integrity of adjacent land. Management challenges in mountain parks are exacerbated by the facts that resources are difficult to document and monitor without specialized access, and that scenic renown draws particularly high numbers of tourists.

Waterton Lakes National Park faces typical management pressures. Its small size makes it particularly vulnerable to human activity on adjacent land to the east, north, and west, although Waterton represents a northern extension of Glacier National Park, Montana, resulting in a large overall protected landmass to the south. The regional ecosystem near Waterton has deteriorated due to the effects of development and disturbance, and the Crown of the Continent ecosystem (the region of the intersection of the continental divide and the 49th parallel) is described as being at risk (Parks Canada 2000). Waterton receives about 375 000 visitors a year (Parks Canada 2000), and striking a workable balance between supporting visitor experiences, contributing to social and economic needs, and maintaining a healthy environment is described as one of the greatest challenges facing managers (Parks Canada 2000). Intense regional human pressure not only makes the protection of land within Waterton Lakes National Park increasingly difficult, but as representative wilderness becomes more rare, the protection of Waterton also becomes more important, with increasingly less room for error.

Waterton Lakes National Park recently formalized its operational priorities in a management plan (Parks Canada 2000). This document outlines a commitment to maintaining certain conservation values through research, monitoring activities and human use management. The park acknowledges the importance of basing decisions on current, scientific information. Park management also adheres to the

principles of precaution and adaptive management, and states that proposals to manage human use will be based upon the best available information.

Scientific investigators, who are in a position to contribute information helpful to park management goals, should take the management priorities and approaches of parks into account when developing information for park use (Bunnell & Huggard 1999). What values is a park interested in preserving? Where do significant gaps in knowledge exist? What activities or approaches will the park consider to achieve its goals? The translation of scientific knowledge to practically-applicable management recommendations requires careful consideration of these questions.

In preparation for this project on the development of management recommendations for non-vascular plant rarity and diversity in Waterton Lakes National Park, Parks Canada objectives were carefully considered with respect to conservation values and organisms of interest, management approaches and goals, research needs, and scales of study and management.

1.4.1 Conservation values

Waterton's management objectives include the following goals (Parks Canada 2000):

> "to maintain biological diversity at broad landscape and community scales, including ecological processes",
>
> "to maintain and restore viable populations of native species…" and
>
> "to protect, maintain or restore rare, vulnerable, threatened, or endangered genetic resources, species and biotic communities".

Thus, key conservation values of which park managers should be aware to make informed management decisions include species richness and species rarity.

Biological diversity and the presence of rare species are among the most common criteria determining conservation value (Margules & Usher 1981). Biodiversity has enjoyed a relatively recent surge of interest (eg. Gaston 1996; Huston 1994) and is central to many current conservation programs (Brockway 1998). Species richness is one popular indicator of diversity that assigns equal value to all species present in a study area, without respect to species abundance or dissimilarity. Margules and Usher (1981) argue against the use of indices that incorporate proportional abundance, and particularly in groups

for which the relative ecological roles of species remain unexplored, it seems artifical to confer greater importance on the basis of great biomass or great rarity. Species richness is demonstrably related to many other aspects of biodiversity (eg. Magurran 1988), and this along with the fact that it is quite simple to measure and understand probably accounts for its widespread use.

Gaston (1997) reviews some of the prevalent definitions of species rarity and acknowledges that rarity in a biological sense usually refers to species abundance or spatial distribution. Species rarity is often evaluated as abundance within a political boundary. The arbitrary position and size of these political units (parks, counties, provinces, countries) often leads to a lack of ecological meaning in resident rare species lists, and rarity as a focus of conservation efforts has often been criticized (Margules & Usher 1981). Practically speaking, however, the conservation of rare species is none-the-less of high priority in many political jurisdictions, and parks nested within provinces and countries must be aware of the provincially- and nationally-rare species dwelling within their boundaries so that their role as preservations for provincial and national resources may be fulfilled. Furthermore, species with low abundance at the park scale are important from the point of view of conserving park diversity since most species in a given study area are rare (e.g. Margules & Usher 1981).

It is difficult to establish patterns of rare species occurrence for predictive purposes because there are by definition very few examples from which to gather data. If one considers rare species as a group (rare species richness), however, patterns may emerge. Lists of rare species for these nested scales may differ from one another due to the relative abundance of a certain habitat type or proximity to a certain dispersal barrier. In these cases, many rare species may be unified by ecological characteristics which may be used to predict their richness.

Unfortunately, devising a broadly-applicable management scheme for an entire park or parks system requires that the 'general rule' take precedence over specific cases, since resources required to document and individually manage all specific cases are not in place (Bunnell & Huggard 1999). Biodiversity and rarity paradoxically *depend* on specific cases, while the general rule is, by contrast, relatively uninteresting both to conservationists and to researchers. Given that many sites must be judged based on predicted conservation value because most sites cannot be fully inventoried, an appropriate

balance between generality (for practical applicability) and specificity (for efficacy) in research and recommendation must be struck.

This balance requires concessions by both the scientists who develop recommendations and the managers who apply them. For example, because rare species occur very infrequently, the exploration of their distribution patterns for the purpose of developing predictive relationships may be considered too frustrating to attempt. Researchers may require significant prior knowledge regarding a species' ecology and may have to sacrifice strictly random (and statistically desirable) sampling schemes in favour of targeting rare habitats to maximize the capture of species of interest. Scientists may further be required to sacrifice the luxury of controlling variables (for example habitat or community type) in favour of making their research broadly applicable within the park. Managers must accept that recommendations developed within a given region are most applicable to that region and cannot necessarily be extrapolated to other parks. The development of recommendations for the protection of park biodiversity requires at least some sampling of biodiversity in all parks in which the management recommendations are to be applied, and the accuracy of recommendations will be improved with increased sampling.

1.4.2 Consideration of 'non-charismatic' species such as non-vascular plants

By acknowledging the overriding importance of ecological integrity, measured in large part by biological diversity (Parks Canada 2000), Waterton Park managers accept responsibility for considering less 'charismatic' taxa such as lichens, fungi, and non-vascular plants (mosses and liverworts) in their management decisions. Nonetheless, inconspicuous contributors to the biodiversity of Waterton Lakes National Park receive little attention, historically and currently, in the Park's management plans (or, to be fair, anyone's management plans). Margules and Usher (1981) concur that "Our naturalist experience will always remain a powerful guide to management actions, but without breadth of thinking we make management recommendations based on our experience with a narrow subset of taxa, potentially at great cost to the rest of biological diversity".

Inventory, monitoring, and preservation of non-vascular plants may present seemingly insurmountable challenges to park managers. They are initially difficult or time-consuming to locate, differentiate, and identify, and there is relatively little public impetus for acquiring this expertise. As a

result, most parks are currently unprepared to protect their non-vascular plants because they do not know which or how many taxa reside within their boundaries, or how human activities are likely to affect them. Tools that simplify the process of identifying and managing these resources can begin to rectify this imbalance. Ecological integrity as measured by biodiversity, the ability of plants to sustain healthy populations, and the sustainable integration of people into the environment, as outlined in the Waterton Lakes National Park Management Plan (Parks Canada 2000), may thus be more reliably addressed in our National Parks.

1.4.3 The nature of human use management

Canada's National Parks Act (1988) declares that "maintenance of ecological integrity through the protection of natural resources shall be the first priority when considering park zoning and visitor use in a management plan". Human use management is defined as "the direction and guidance of people – their numbers, their behaviour, activities, and the infrastructure they require", and constitutes a major activity required for the preservation of ecological integrity in Canadian National Parks (Parks Canada 2000).

Management actions such as "relocating trails…removing trail signs and trail head facilities, relocating backcountry campgrounds" and the application of wilderness, special preservation, and recreation zone designations (for example) require knowledge of ecological impact at site or zone scales. Where the presence of particular conservation value is documented, park managers can direct human activity to less sensitive sites. For the vast majority of a park's land base, which remains botanically unexplored, basic patterns of conservation value could be predicted based on inventoried land. Patterns based on readily-identifiable habitat or climate features can create surrogate cues for time-pressed management personnel. The accuracy of these predictions could be continually improved upon as inventory and monitoring efforts progress.

1.4.4 Research needs: Inventory, monitoring, and the interpretation of floristic data

To compromise effectively among competing land uses, conservation values must be evaluated and prioritized (Margules & Usher 1981). Inventory remains the best way to gather information

contributing to these evaluations – without knowing what resources are present within a park, how can it be possible to rank their importance?

A key action designed to maintain conservation value within Waterton is to "monitor changes in the abundance of plant and animal species [and to] evaluate management decisions that influence those changes" (Parks Canada 2000). Furthermore, the park proposes to "monitor and report on the status of plants that are rare, endemic, or at the edge of their range." Monitoring implies some knowledge of resources. This kind of benchmark or baseline data is usually derived from inventory work. Inventories can also provide a basis for the patterns used to predict the value of uninventoried land.

Parks benefit from inventory and monitoring data in several ways. Most directly, the discovery of species occurrences allows managers to direct human activity away from species of conservation interest and their habitats. However, data can be explored in many ways to provide managers with clues as to what features within park boundaries are of conservation interest, and how to manage park land that has not yet been inventoried. Comparing a park's flora to that of adjacent regions helps to reveal what floristic characters are unique to the jurisdiction, and what characters are protected in adjacent parks. The role the park plays in preserving provincial, national, and global diversity is demonstrated. Within the park, patterns of species occurrence with respect to geographic and environmental data, which are often more readily acquired than inventory data can help managers to direct human activity away from sites that are *likely* to support high conservation value. The research tools required for these kinds of explorations are in place, since the causes of species richness hold the intense interest of plant ecologists, yet these studies often fall short of declaring their management implications.

1.5 Significance of bryophytes in mountain ecosystems

Bryophytes, or non-vascular plants, are defined in part by having a gametophyte generation that is dominant, conspicuous, and free-living, with sporophytes that depend upon the gametophytes throughout their existence. Bryophytes require free water for fertilization, and are thus usually small in stature compared to most vascular plants. Their size helps to account for their unique ecology and widespread occurrence on earth, because it allows plants to be distributed with respect to microhabitats (e.g. Geissler

1982) rather than the macroclimate to which most other terrestrial vegetation is so closely bound. Mosses are the most readily identified and hence widely known group of non-vascular plants.

The ecological importance of bryophytes has been reviewed by several researchers (Longton 1992). Bryophytes are important in primary and secondary successional contexts, being among the first organisms to colonize newly-exposed and freshly-disturbed substrates. Many bryophytes are dessication-tolerant, tenacious, slow-growing organisms well-adapted to 'inhospitable' substrates with slow nutrient-release rates. Their colonization facilitates the establishment of higher plants by weathering their substrates, accumulating organic matter, and concentrating nutrients. Conversely, in other situations, mosses cover surfaces that may otherwise be weathered by erosion and insulate surfaces that may be weathered by frost, and their presence may retard the germination and establishment of vascular plants (During & van Tooren 1990). They stabilize soil temperature and moisture and affect substrate chemistry. Regardless of whether their influence is positive or negative, bryophytes help to shape the nature of the communities in which they live.

The role of bryophytes is particularly critical in climatically-severe habitats that do not support "higher" plant life, where mosses and lichens constitute the climax plant community. Bryophytes dominate certain kinds of peatlands and tundras, accounting in these situations for the bulk of biomass production and nutrient cycling. In some boreal forests, their biomass exceeds the above-ground production of trees (Oechel & Van Cleve 1986), and their ability to exchange cations places them in key moisture retention and nutrient absorption roles. In the plant kingdom, bryophytes are second only to vascular plants in diversity, and they participate in competitive and facilitative interactions characteristic of all plant communities. Bryophytes also provide food and shelter to a wide variety of animal species.

Several characteristics that make mosses important in terrestrial ecosystems are particularly applicable to their role in mountain settings. For example, mountainous regions encompass habitats characterized by extreme climate and exposed, unstable, rocky substrate, where bryophytes are among the few taxa that can survive. Auto-succession, a condition of inhospitable habitats in which pioneer and climax communities are the same, was first described in alpine Scandinavia. Körner (1999) emphasizes the "decoupling" of low stature vegetation from macroclimatic conditions through the accumulation of heat in the canopy and associated top soil during sunshine hours. Of all life forms, this effect is greatest in cushion

plants. Many colonies of acrocarpous moss species display a "cushion" growth form (e.g. *Bryum* spp.). Mosses thus avoid many of the climatic stresses which may limit the distribution of other, larger organisms (Geissler 1982). Furthermore, the dessication tolerance of mosses (e.g. *Schistidium* spp.) accounts for the role they play as colonizers of substrates newly-exposed by rock-fall, deglaciation, and alluvial deposition, all of which are particularly active in mountain environments (Tivy 1993). These natural adaptations allow the altitudinal range of mosses to exceed that of vascular plants.

Geissler (1982) reviewed knowledge (largely pertaining to the Alps) of mountain bryophyte communities, and stressed that bryophytes dominate in certain wet and dry communities, both as pioneer vegetation and at later stages of succession. Furthermore, Longton (1984) and Slack (1988) have emphasized the importance of bryophytes in undisturbed ecosystems, and mountain habitats tend to be affected less by human activity than others. Low-stature bryophyte species may provide the "minimum soil coverage" required to establish erosion protection, frost protection, nutrient cycling, and water vapour discharge for less-resilient, taller vascular plants at high altitudes (Körner 1995). In this capacity they are critical contributors to biodiversity and ecological integrity high on mountains.

The small stature of bryophytes has also led to a long history of neglect. Margules and Usher (1981) describe the prevalence of disproportionate interest in conspicuous species leading to an imbalance of knowledge and conservation effort. Cox and Larson (1993) report that the misconception that lichens and bryophytes are ecologically and economically unimportant has lead to their exclusion from ecological studies. The size of bryophytes also tends to intimidate researchers, and few taxonomists are trained in their identification. Mountain bryophytes may be especially challenging: Geissler (1982) emphasized the importance of vegetative propagation under climatic conditions that impede the consistent production of spores, and the taxonomic difficulties resulting from the lack of sporophytes in combination with wide environmentally-induced variation of available characters. Interest, education, inventory, and the development of tools that facilitate the incorporation of bryophytes into management activities are sorely needed.

1.6 Definition of terms

Bunnell and Huggard (1999) deplore the poor definition of many terms critical to establishing clear communication between researchers and managers. The following definitions were applied in this study, with consideration to the ways in which they are applied in management documents and in field-specific literature:

Biological diversity / Biodiversity / Diversity – In this study, diversity is measured as species richness.

Habitat – The concept of habitat in this investigation follows that of 'meso-habitat' as described by Vitt and Belland (1997). Habitats are distinguished from each other based primarily on overstory vegetation, site moisture, and dominant substrate. Habitats may be any size, as long as the conditions defining them persist. Examples of habitat types include coniferous forests, forested cliffs, stream beds, and talus slopes.

Microhabitat – Mosses perceive their environment on a microhabitat scale. Thus, in this study, microhabitats are small habitat features, defined by substrate, moisture, and light conditions, capable of supporting one to several moss colonies. Examples include the tops, sides, and bases of decaying logs, crevices in cliffs, and exposed mineral soil.

Region – In this study 'region' refers to the scale of a park, or of a park and its immediate environs.

Site – Sites are defined, for sampling purposes, at the scale of habitats. Where a habitat is too large to be sampled entirely, a site is established within the habitat.

1.7 Thesis objectives

The ways in which the flora of Waterton is set apart from that of the region, province, or country in which it occurs provide clues to the relative importance of park elements to larger-scale preservation issues. The latter objective serves to aid managers in site-by-site or area-by-area conservation decision-

making. The ways in which the diversity and rarity of Waterton's mosses are distributed with respect to Waterton environments, habitats, and communities provides clues to the relative value of individual sites with respect to management goals.

The following study supports Parks Canada's commitment to ecological integrity, scientifically-based management, and the need for integration of people and a sustainable environment by:

a) providing an inventory of non-vascular plants to provide a baseline for monitoring and documentation of biological diversity resources;

b) evaluating non-vascular plant diversity in the context of the surrounding regions to allow park managers to assess the conservation value of their jurisdiction with respect to others and to prioritize conservation goals; and

c) describing patterns of non-vascular plant conservation value within the park to help managers make human use management decisions that uphold management priorities on un-inventoried land.

These actions will help managers to identify, prioritize, and protect a poorly-understood and under-represented biological resource despite intense competition for time and money within the Park.

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2. MOSS FLORISTICS AND PHYTOGEOGRAPHY OF WATERTON LAKES NATIONAL PARK IN THE CONTEXT OF THE NEARBY ROCKIES

2.1 Introduction

The conservation of natural biodiversity is widely accepted as critical to the long-term sustainability of natural resources. Floristic investigations underpin plant biodiversity conservation by discovering a region's resident plant taxa and comparing them to the taxa of other regions. Such comparisons aid quantitative assessments of the relative significance of floras, and may be correlated with regional comparisons of environmental and historical factors to explain temporal and spatial change in biodiversity. These functions are central to biodiversity conservation because they provide sound guidance for the assignment of land management priorities.

The floristic similarity and distinction of parks and regions can be assessed in many ways. Similarity indices allow phytogeographers to numerically summarize the number of shared presences, shared absences, and/or mismatches of species in two regions (e.g. Faith 1983; Jaccard 1912; Sneath & Sokal 1973). Nekola and White (1999), for example, explored the relationships between geographic distance, habitat and species type, and floristic similarity, using Jaccard's similarity index. Non-quantitative comparisons of the *nature* of species (e.g. morphology, phytogeography, climatic affinity) in different floras can help to reveal the mechanisms underlying numerical differences and to interpret features unique to a particular flora. This approach has been used by Vitt and Belland (1997), who also employed separate consideration of the rare flora of different regions to augment their understanding of species distribution patterns in Alberta. Applying the same type of analysis at the scale of parks within a region can help to quantify and characterize the conservation values protected by adjacent jurisdictions, and to suggest climatic and historical factors accounting for species distributions.

Mountain ecosystems support greater plant diversity than the surrounding lowlands (Tivy 1993). The high elevation of mountain tops makes them biogeographically important as barriers to species dispersal and as glacial refugia – centres of species persistence during glaciation and of recolonization following recession of the ice sheets. High peaks are interspersed with low valleys and plains, leading to an extreme geographic concentration of habitats with radically varying elevation, aspect, wind exposure, and precipitation. Mountain formation, which causes many geologically distinct layers of the earth's crust

to be exposed, superimposes substrate variability across these complex climate gradients, creating infinitely variable plant habitats.

The northern Rocky Mountains represent a concentration of diverse habitats compared with the prairie and boreal lowlands to the east and west. They are home to numerous protected areas including National Parks, which preserve increasingly rare natural landscapes amidst accelerating resource development on adjacent lands. Waterton Lakes National Park ('Waterton'), Alberta, the smallest of Canada's Rocky Mountain National Parks, features an uncommon richness of vascular plant species, and supports including unique species compared with floras of adjacent regions of the Rocky Mountains (Ogilvie 1962; Kuchar 1973; Kuijt 1982). Remarkable features of the vascular plant flora of Waterton remains unexplained, but most authors suggest unique factors in history, climate, geology, and physiography (eg. Breitung 1957; Ogilvie 1962; Kuijt 1982).

These factors cannot be expected to influence the vascular flora exclusively – mosses, recognized for their key roles in nutrient cycling, successional change, and animal habitat, are notorious for their affinity for specific habitat conditions. Mosses are generally poor regulators of internal moisture (Schofield 1985) and lack the roots that allow vascular plants to exploit resources beyond the point of their attachment to the substrate. Mosses have little protection against changes in climate, chemistry and other edaphic conditions, but the small stature of most species allows them to take advantage of extremely localized patches where favourable conditions coincide. The complex, interacting habitat gradients characteristic of mountain ecosystems in general provide ideal conditions for high moss diversity. Furthermore, adaptations to ectohydricity allow many moss species to occupy very cold and dry habitats in which vascular plants cannot thrive (Schofield 1985). Mountain peaks exemplify this kind of habitat extreme.

Mosses are underexplored throughout the Canadian Rocky Mountains, but some parks have received relatively greater scientific attention. Even in these regions, collection records from diverse field trips and studies have rarely been compiled to provide even preliminary indications of diversity and other floristic resources.

The objectives of this investigation are:

1) to characterize the moss flora of Waterton Lakes National Park,

2) to determine the floristic affinities and distinctions of the Waterton moss flora in the context of nearby Rocky mountain regions, and

3) to relate the floristic character of Waterton's moss species to patterns documented for the vascular plant flora

2.2 Study areas

Waterton Lakes National Park, a relatively small (530 km^2) mountain park in the extreme south-west corner of Alberta, Canada (Figure 2.1), was established in 1895. It is bounded in the west by the British Columbia border, which coincides with the continental divide. The southern park boundary is the Canada-United States border, across which Waterton is contiguous with its American counterpart, Glacier National Park, Montana. Within Waterton, mosses were collected and studied intensively.

Five additional Rocky Mountain regions (Figure 2.1) both east and west of the continental divide (Table 1) near Waterton were used to place the park in a regional floristic and phytogeographic context: Glacier National Park ('Glacier'), Banff National Park ('Banff'), Jasper National Park ('Jasper'), Willmore Wilderness Park area ('Willmore'), and the region encompassing Kootenay National Park, Yoho National Park, and the Kinbasket Lake area ('West Slopes'). These areas vary in size and jurisdiction (Table 1) occurring in Montana, United States of America, and in Alberta and British Columbia, Canada. The regions of study are generally protected from development and were selected because they represent focal points of botanical and ecological study. No region of the Canadian west slopes (British Columbia Rockies) has been studied to the extent of the National Parks of the more accessible east slopes (Alberta Rockies). However, floristic affinities between the vascular flora of British Columbia and that of Waterton Lakes National Park made comparisons east and west of the continental divide especially desirable, so records for the three British Columbia regions were combined to form a general West Slopes flora. Sixty percent of Glacier National Park also lies west of the continental divide, but is not considered separately because separate checklists for east and west parts of the park were not available.

2.2.1 Climate

The climate of individual parks has been documented to varying extents with particularly little climate data collected in or near Willmore Wilderness (but see Alberta Wilderness Association 1973 for some description). Climate studies of various Rocky Mountain regions (Finklin 1986, Poliquin 1973 (Glacier, Waterton); Holland & Coen 1982 (Banff, Jasper); Janz & Storr 1977 (Banff, Jasper, Kootenay National Park, Yoho National Park); Achuff et al. 1982 (Kootenay National Park)) generally conclude that marked spatial climate variation unifies the study area. The slopes that differentiate the mountains from the adjacent flat forests and plains provide a variety of elevations, aspects, and topography (Daubenmire 1943; Breitung 1957; Poliquin 1973; Tivy 1993) in close proximity. These, in turn, produce an unparalleled diversity of local climates by affecting insolation intensity and duration, temperature, cloud cover, precipitation, hydrology, nutrient balance, and substrate chemistry (Daubenmire 1943; Poliquin 1973; Tivy 1993). Mountain tops throughout the study area represent climatic extremes.

Precipitation varies widely within the park (Finklin 1986), generally increasing closer to the continental divide and at higher elevation. The annual precipitation of 1300 mm at some Waterton locations on and near the continental divide (Lopoukhine 1970) represent Alberta's highest precipitation total (Kuijt 1982). Thirty percent of the annual precipitation falls in May, June, and July (Breitung 1957) with a peak in the first half of the growing season (Kuijt 1982). Annual precipitation minima occur in July and August. At least 60% of annual precipitation falls in winter (Poliquin 1973), amounting to an average acumulation of 2550 mm. Snow persists into late summer at high elevations (Breitung 1957; Lopoukhine 1970). On leeward slopes, particularly in depressions or treed places, where great accumulation occurs, complete snowmelt may only occur every few years (Breitung 1957). No glaciers occur in the park.

Less thunderstorm activity occurs in Waterton as compared with parks to the north, resulting in a relatively low incidence of fire. Weather systems in Waterton usually result from travelling low pressure systems carrying Pacific moisture (Poliquin 1973). A storm track over the 49th parallel is reported to have a maritime influence on the local climate of Waterton, particularly on west-facing slopes (Daubenmire 1943; Hansen 1948; Ogilvie 1962; Lopoukhine 1970). Daubenmire describes the climate of the northern Rockies in the vicinity of the 49th parallel storm track as "similar to that of the west slope of the northern Cascades", and Finklin (1986) states that the climate of Waterton-Glacier is transitional between northern Pacific coast

and continental climates. Waterton and Glacier thus display greater annual precipitation, more amplitude in seasonal precipitation, and warmer temperatures than areas to the north (Ogilvie 1962).

Large seasonal and diurnal temperature fluctuations are common, as periodic warm chinooks punctuate the prolonged influence of arctic air masses in winter (Breitung 1957; Poliquin 1973). Mean minimum winter temperatures are higher than those of mountain parks to the north. The growing season begins around May 20, and lasts until September 10 (113 days), and July and August are generally frost-free (Poliquin 1973). On an average of nineteen July and August days, the temperature rises above 21°C, and maximum daily temperatures often exceed 30°C (Poliquin 1973). These constitute some of the highest temperatures recorded in Alberta (Breitung 1957).

Wind is described as one of the most important climatic elements of the Waterton region (Poliquin 1973). Strong prevailing west or southwest winds (Breitung 1957; Poliquin 1973; Kuijt 1982) contribute to the dry summers, but peak during the winter months (Kuijt 1982). Local variation in physiography produces some variation in wind direction (Finklin 1986).

Most climatic characters throughout the northern Rockies are similar to those described for Waterton. Despite this pervasive, complex, mountain climate, certain broad climatic gradients exist, leading to significant differences between levels of latitude along the Rocky Mountain cordillera and between the west and east slope of the continental divide.

2.2.1.1 Latitudinal climate variation

Parks at different latitudinal positions receive (in general) different amounts of solar energy in different seasons (Janz & Storr 1977). Thus mean annual temperature is the main climatic factor varying latitudinally along the Rockies (Daubenmire 1943; Janz & Storr 1977). Generally speaking, isotherms of mean temperature decrease in altitude toward the poles at an average rate of 30 m per 15 minutes of latitude (Hopkins 1938 in Daubenmire 1943).

The Rocky Mountains lie perpendicular to the direction of prevailing winds in the upper atmosphere (Janz & Storr 1977). Storm tracks centred over specific latitudinal zones such as the one over Waterton (Daubenmire 1943; Janz & Storr 1977) can alter local climates by creating "peninsular" shaped extensions of coastal climate farther inland than occurs at latitudes unaffected by strong, prevailing

westerly winds (Daubenmire 1943). Daubenmire (1943) also reports another storm track in the central part of Alberta's Rocky Mountains, but does not consider it to be a major route. The influence of pacific air is also modified by latitudinal variation in the number of mountain ranges pacific air must cross to reach each Rocky mountain region and in the distance between the Rockies and the Pacific Ocean.

2.2.1.2 Longitudinal climate variation

Although the climates of all the regions in this study are classified as "continental", the continental divide represents a major climatic boundary in the Rocky Mountains, owing to its high elevation and orientation perpendicular to prevailing atmospheric winds (e.g. Janz & Storr 1977). Moisture carried by westerlies is precipitated west of the divide, leaving the east slopes in a dry rain shadow characterized by significantly less precipitation distributed with different seasonal emphasis (Daubenmire 1943). Summer and winter precipitation are generally more equal east of the divide and warm chinooks melt snow more quickly, whereas winter precipitation dominates and persists for longer intervals in the west (Daubenmire 1943).

Daubenmire (1943) reports that winter temperatures on the west slopes are moderated under the influence of west winds moving inland from the coast compared with temperatures east of the divide. West Glacier (Montana) records higher mean temperatures than stations east of the Divide in the southern Rockies (Poliquin 1973). Janz and Storr (1977) attribute significantly higher winter temperature minima in Kootenay and Yoho National Parks (-43°C) as compared with Banff and Jasper (-50 °C) to the protection the continental divide provides against the influx of arctic air from the northeast. Chinooks, conversely, cause much higher winter temperature maxima east of the Divide, resulting in a slightly wider winter temperature range.

2.2.2 Physiography, geology, and soils

Waterton occupies the foothills and eastern Front (Lewis) Ranges of the Rocky Mountains (Table 1). Waterton's mountains were formed when large slabs of sedimentary rock were tilted and pushed in approximately an eastward direction (Kuijt 1982). The flat or shallow orientation of the Lewis thrust leads to the unique situation that old rock (sedimentary rock formed long ago) overlies recent formations. The

foothills in this part of the Rockies share their structure and rock types with regions to the north, but they display a very different form (Harrison 1976): their slopes are extremely shallow, so that they more closely approximate the physiography of the adjacent eastern plains. Eastward movement of the mountain land mass overtook much of the foothills landforms (Baird 1964), leading to an abrupt transition between mountains and prairies. The mountains of Banff, Jasper, and Willmore Wilderness, in contrast with Waterton, appear in long, parallel rows that reflect the *upward* movement of the earth's crust on steep faults.

Twenty-three percent of the area of Waterton consists of exposed bedrock (Lopoukhine 1970). Main rock types in Waterton are sedimentary: Precambrian and lower Paleozoic red shale, slate, sandstone, and limestone (Poliquin 1973; Lopoukhine 1970; Kuijt 1982). The red shales distinguish these mountains geologically from those to the north (Kuijt 1982). In between some sedimentary layers are thin 'injections' of igneous rock (Baird 1964). Thus calcareous chemistry predominates with rare acidic pockets. Waterton's prairie component is underlain by thick glacial debris over Cretaceous and Tertiary sandstone and shale (Lopoukhine 1970; Kuijt 1982). All Rockies are dominated by calcareous rock.

McKay (1952) reports that Waterton comprises no formations of the Palaeozoic era, distinguishing it from mountain parks on the east side of the Rockies both north and south of the park. The sediments that compose much of the bedrock are identical in character and sequence to those west of the Flathead River, west of the continental divide, and form the south-eastern limit of a western land mass (McKay 1952).

Glaciation in and near the mountainous land formed by the Lewis overthrust added physiographic diversity by shaping low rolling prairies, high cirques, large lakes, and deep valleys (Breitung 1957; Poliquin 1973; Kuijt 1982). Small snow-fed lakes in high basins drain into the Waterton River by way of successive waterfalls and streams (Breitung 1957; Kuijt 1982). The ancient rock exposed by the Lewis overthrust is extremely hard, leading to steeper valleys and greater relief than mountains derived from younger material (Harrison 1976). In the Waterton area the young rock overlying the older layers has eroded from the hard rock at the base of the overthrust (Harrison 1976). Talus slopes, rock slides and fresh screes give evidence of rapid weathering (Breitung 1957).

Most soils in Waterton are derived from calcareous parent material and have undergone podzolization (Lopoukhine 1970). Peatlands and black soil exist in low quantity in the east part of the park

(Lopoukhine 1970). Soil weathering is limited because runoff from snowmelt at high elevations is very cold (Lopoukhine 1970).

2.2.3 Vegetation and flora

Vegetation (referring to the general patterns and structure of dominant plant communities) mirrors climate in its complex spatial variability throughout the northern Rockies. The effect of climatic variables associated with elevation is particularly obvious in mountain vegetation, with more localized climate and physical factors modifying these patterns. Daubenmire (1943) describes altitudinal vegetation zones in detail, and Habeck (1987) describes generalized vegetation patterns in the northern Rockies. In Waterton three principle vegetation types are recognized: two treeless zones at high and low elevation extremes with an intervening forest zone (Breitung 1957; Poliquin 1973; Kuijt 1982). At low elevations, wetlands and dry grassland predominate. Wooded vegetation is scarce due to drought and high temperatures (Lopoukhine 1970), and is restricted to Poplar (*Populus*) groves and of pure thickets of Willos (*Salix*) and Birch (*Betula*). Higher up, even-aged stands of lodgepole pine (*Pinus contorta,* the most common tree species in the park (Poliquin 1973)) form a disturbance-regulated mosaic with patches of Engelmann Spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). At least two thirds of the mountain slopes are covered by coniferous forest (Breitung 1957). Shrub-covered avalanche slides often interrupt forest vegetation, particularly on south-facing slopes (Breitung 1957). Stunted limber pine (*Pinus flexilis*), white-bark pine (Pinus albicaulis), and subalpine fir occur above the coniferous forest, and decrease in height and density with increasing elevation until trees are represented only in krummholz form. Timberline occurs at approximately 2100 m (Breitung 1957), above which low temperatures, wind, snow, and other factors inhibit tree growth (Lopoukhine 1970). Open herbaceous meadows at high elevations grade into alpine semidesert consisting of rocky meadows and ridges of varying stability.

Similar patterns are seen in all other mountain regions in this study, although some geographical patterns are seen. Daubenmire (1943) and Tivy (1993) describe a progressive decrease in the altitudinal limits (and, as each zone reaches the basal plain, progressive decrease in the altitudinal breath) of vegetation zones (including tree line and snow line) with increasing latitude, being roughly correlated with 10 degree isotherms for the warmest month. Timberlines are also often elevated toward the interior of

continents and individual mountain ranges (Tivy 1993). Warm chinooks cause 'redbelt' injury to coniferous vegetation at certain elevations east of the continental divide (Robins & Susut 1974). Vegetation itself modifies local climate, making the habitats of species that grow below the canopy even more complex.

Waterton is home to a unique and rich suite of vascular plant species, or 'flora' (Breitung 1957; Kuchar 1973; Kuijt 1982). Fifty-five percent of the province's vascular plant species (Kuijt 1973) including over half of Alberta's rare vascular species (Ogilvie 1962; Kuchar 1973) exist within less than 0.1% of the province's area (Kuijt 1973). Prairie, boreal, arctic-alpine, Cordilleran, endemic, cosmopolitan, and exotic species are represented (Kuchar 1973). Waterton lies directly south of an unexplained "botanical watershed" for vascular plants, running east-west at approximately 50° latitude (Ogilvie 1962; Kuijt 1982) which floristically isolates Canada's southernmost Rockies from the northern remainder. Of vascular species found south of the 'watershed', many are Cordilleran in their gross distribution (Ogilvie 1962; Kuijt 1982): about 100 species of the cedar-hemlock association of central British Columbia and the adjacent United States cross the continental divide and reach their eastern limits in Waterton and Glacier Parks (Hansen 1948; Lopoukhine 1970). Another suite of vascular groups are found in British Columbia and the Cypress Hills or in the Rockies both north and south of Waterton, but show coincident distributional gaps or extreme rarity in southern Alberta (Kuijt 1982).

The bryophyte flora of Waterton is much less studied. Bird (1968a, 1968b, 1969a, 1969b), Hermann (1969), Kuchar (1973) and Stringer (1966, 1969) are the principle contributors to the previous list of 149 moss species known for the park. Approximately 500 mosses are known for Alberta (current study). Several other bryophyte studies, though not undertaken specifically in Waterton, are relevant to the current investigation (Bird 1962; Bird & Hong 1969). Harsh high-elevation habitats are suitable for pioneer species that are adapted to drought, cold, and high solar radiation, and that are unable to compete with forest species of lower elevations. The phytogeographic affinities and rarity of Waterton mosses have not previously been analysed (but see Vitt & Belland 1997).

The remaining Rocky Mountain regions in this study seem not to have benefitted from comprehensive works such as those of Kuijt (1982) for Waterton, nor the scientific curiosity that inspired speculation as to the origins of theWaterton flora. Species lists are available in ecological land

classification documents (Achuff et al. 1984; Holland & Coen 1982), in addition to some field guides and identification manuals. Standley (1921) lists plants in Glacier. Daubenmire (1943) recognizes four floristic zones of the Rocky Mountains, the most northerly two of which are included in the current investigation. Daubenmire's 'northern Rockies' (central Wyoming to central Alberta and British Columbia) are typified by woody plants such as western larch (*Larix occidentalis*), devil's club (*Oplopanax horridum*), whitebark pine (*Pinus albicaulis*), western white pine (*Pinus monticola*), and western yew (*Taxus brevifolia*), most of which preferentially inhabit the regions west of the Continental Divide. The 'far-northern Rockies' are characterized by the presence of black spruce (*Picea mariana*) and an absence of narrow-leaved cottonwood (*Populus angustifolia*). Relict and endemic vascular plants are more common in mountain environments, where their populations have become isolated from more continuous distributions which prevailed in earlier climates (Körner 1995, 1999), suggesting that each Rocky Mountain park should posess some unique floristic characters.

2.3 Methods

2.3.1 Moss collection and identification

The habitat types within Waterton Lakes National Park were identified using published accounts (Kuchar 1973; Lopoukhine 1970) and field reconnaisance (Table 2.2). At least four sites representative of each type (total 112 sites) were selected with reference to vegetation maps (Achuff et al. 1997), but primarily by field reconnaisance. Strictly anthropogenic habitats were excluded from the study, although several sites were influenced by human activity. The level of detail (Table 2.2) applied to habitat definitions encompassed almost all habitats observed in the field and allowed an appropriate number of representative sites to be sampled in the time available. Because species capture was of paramount importance, maximizing the park area covered and variability within habitat types were primary criteria. In the summer of 1997, representative microhabitats within each site were examined until no new moss species were found (McCune & Lesica 1992; McCune et al. 1997; Newmaster et al. 2000). Species identification generally followed the concepts of Lawton (1971), with additional reference to Crum and Anderson (1981), Horton (1983), Koponen (1974), Peterson (1979), Shaw (1982), Spence (1988), and Syed (1972) for certain taxonomic groups.

Approximately 4500 bryophyte collections were made in Waterton in the 1997 field season. These were supplemented with fewer than 100 incidental collections in the summers of 1998 and 1999. Voucher specimens are stored in the University of Alberta Cryptogamic Herbarium (ALTA).

2.3.2 Compilation of species lists

Species lists for the six Rocky Mountain study areas were compiled using a combination of published reports and herbarium records. Some species records for all study areas were obtained from databases maintained by R. Belland at the Devonian Botanic Garden, University of Alberta. The database includes largely the collections of Dr. D.H. Vitt, and specimens curated at the University of British Columbia. These lists were supplemented in the following ways:

1) Glacier records reflect Hermann (1969), with additional records compiled by Park staff (Tara Williams (Ecologist, Glacier National Park), personal communication).

2) Waterton records additional to collections made in 1997 were gleaned from Kuchar (1973), Cheryl Bradley (unpublished), and Vitt (unpublished), as well as from herbarium records at ALTA and the Provincial Museum of Alberta (PMA).

3) The initial list for Banff was taken from the Ecological Land Classification (Holland & Coen 1982), after which all Alberta species not listed for Banff were investigated at ALTA and PMA, and added where necessary.

4) Belland (2000) produced a comprehensive list of mosses for Jasper National Park after exhaustive literature and herbarium searches, and this list (with few taxonomic alterations) was used for that park.

5) Willmore/Grande Cache records were supplemented with reference to Vitt and Koponen (1976) and to records from ALTA and PMA.

6) The west slopes lists drew data from Ecological Land Classification documents (Achuff et al. 1984; Coen 1982).

The species identies of collections from Glacier, Banff, Jasper, Willmore, and West Slopes were not verified (in this study) in most cases, although some suspect and inaccessible specimens were excluded from the lists. This study did not include an exhaustive study of herbarium records outside Alberta, and

these combined with the hundreds of undocumented collections currently awaiting identificaton and curation will extend the published species lists for all regions, particularly those outside the province. Furthermore, the eastern slopes are generally more accessible than areas west of the divide, leading to less complete British Columbia collection records. This study must therefore be regarded as one early phase of a continually evolving understanding.

Nomenclature was standardized to the North American checklist (Anderson et al. 1990), with a few exceptions. *Amblystegium juratzkanum* Schimp., *Brachythecium asperrimum* (Mitt. ex Müll. Hal.) Sull., and *Grimmia dupretii* Thér. were accepted as distinct taxa in this study due to their distinct morphology and historical recognition by collectors. Neither *Campylium calcareum* Crundw. & Nyholm nor any of its synonyms appear on the North American checklist, but it appears to be a widely accepted taxon. *Dicranum sulcatum* Müll. Hal. was retained for the same reason. Compilation of species lists resulted in the expansion of floras for all regions, as well as an increase in the number of species known from Alberta. The Alberta flora used in this study is comprised of the provincial list published by Ireland et al. (1987) with additions from this study.

2.3.3 Floristic and phytogeographic analysis

The flora of Waterton was described in terms of the climatic affinities, distributional continuities, morphologies, and rare species represented in its flora. Climatic affinities – arctic-alpine, boreal, cosmopolitan, montane, and temperate - refer to the broad-scale affiliation of species (or lack thereof, in the case of cosmopolitan species) with different vegetation biomes, and were modified from Belland (1987). The extent and pattern of the world distribution of boreal, temperate, and montane species was sub-classified as continuous, disjunct, or endemic (western North America, or broader North American endemism). Each species was classified morphologically as acrocarpous or pleurocarpous, according to the position of the sporophyte.

Rare species, or species with very sparse or spatially limited regional distributions, are of particular phytogeographic significance and conservation value. Rare species in this study were defined by their presence on Alberta Natural Heritage Information Centre (ANHIC) tracking lists, which have twenty

or fewer known occurrences (separated by at least 1 km) in Alberta. Species new to the province as a result of being listed in this study were treated as tracked species. ANHIC rarity classifications cannot be accurately applied to the west slopes and Glacier because many species that are rare in Alberta are at the edge of ranges centred to the west or south of the province. A second set of rare species – comprising species that occur in only one region out of the investigated six - was also examined to capture rarity on the scale of the focal regions of this study, although the abundance of each species in each park is not known.

The affinities and distinct characters that place the Waterton moss flora in the context of the nearby Rocky Mountains were identified by comparing the Waterton species list with lists of moss species for each of and combinations of the other five Rocky Mountain regions. Similarities and differences between regions were evaluated

a) by determining the number of shared and un-shared species. Jaccard similarity co-efficients were calculated for all pairs of regions. Nekola and White (1999) and Rice and Belland (1982) recommend Jaccard's index as it is simple and easily related to other binary similarity indices. Faith (1983) demonstrates some shortcomings of the Jaccard Index, but points out that it is appropriate when proportional differences are of interest, and when the proportion of species matches to mismatches is important - as they are in this study. Sorenson's Index was also applied in this study and yielded equivalent results. Thus, results for Jaccard only are presented here.

Monte Carlo simulations were used to generate thirty sets of six moss floras composed of species drawn randomly from a species pool of all species in the current study, represented at frequencies identical to the species in the current study. Jaccard similarity indices were calculated between pairs of randomly-generated floras for each set. Mean similarity index and standard deviation for the thirty iterations of each pair provided 95% confidence intervals against which similarity indices between pairs of actual floras could be compared (Rice & Belland 1982; Belland 1989). This procedure allows one to determine whether or not a calculated similarity index differs significantly from one derived from random floras. Without this context, similarity indices cannot be reliably evaluated (Rice & Belland 1987).

b) by determining the number of species exclusive to a flora or shared exclusively by a set of regional floras, as evidence for floristic distinction of (a) particular region or regions.

c) by visualizing floristic similarities among the study regions through Correspondence Analysis (Ter Braak 1986, 1994) on presence/absence data for the six full regional floras.

d) by comparing regional representation (in terms of species richness) by species of different climatic affinity (boreal, temperate, montane, arctic-alpine, cosmopolitan), and distributional continuity (continuous, disjunct, endemic) in their global distribution. Representation by different morphological affinities (acrocarpous and pleurocarpous growth habit (Schofield 1985)) and the number of rare species in each flora were also compared. To correct for varying regional richness (unknown proportions of which results from variability in sampling area and effort), the number of species representing a given affinity was expressed as a percentage of each local flora. This approach was adopted with the assumption that new species discovered in all regions would reflect the floristic affinities of the documented flora. This assumption does not account for the tendency of collectors to avoid certain groups (e.g. *Bryum*) of difficult-to-identify and/or inconspicuous taxa.

Affinities and regional similarities and differences of the Waterton moss flora were compared with patterns observed by previous researchers for vascular plants.

2.4 Results

Regional floras are listed in Appendix A. The current species list for Waterton of 288 mosses (Table 1) includes about 58% of the 499 Alberta moss species recognized in this study within less than 0.1% of the province's area. The field portion of this study almost doubled the number of moss species published for Waterton (Kuchar 1973), but failed to detect twenty species reported by other researchers (Bradley unpublished; Kuchar 1973; Vitt unpublished) (e.g. *Buxbaumia viridis, Ditrichum montanum, Desmatodon obtusifolius, Dichelyma uncinatum, Sphagnum girgensohnii, Thamnobryum neckeroides*). The floras of individual parks in this study varied from 226 in Willmore to 344 in Jasper (Table 1). Despite the varying sampling efforts Waterton appears to display an exceptionally high number of species (and

species of different affinities) per unit area compared with other regions in this study. The six regions studied included a total of 489 moss species.

2.4.1 Climatic affinities

The greatest proportion of Waterton mosses (56%) are boreal in global distribution (Figure 2.2). Temperate species account for 15% of Waterton mosses, and montane species make up 11% of the Waterton moss flora. Nine percent are cosmopolitan species. The smallest proportion of Waterton moss species (7%) are arctic/alpine species. The climatic affinities of the remaining 2% of Waterton species are unknown.

In all regions, the largest proportion of the non-cosmopolitan flora was boreal, followed by temperate species (Figure 2.2). In Waterton, Glacier, and West Slopes, montane species represented the third largest fraction, whereas arctic-alpine species exceeded montane species in Banff, Jasper, and Willmore. The combined flora for all six regions featured patterns of climatic affinity similar to Waterton, Glacier, and West Slopes. When the entire moss flora for the six regions is considered, a smaller proportion of the species is of boreal (51.5%) and cosmopolitan (5.7%) affinities than in each regional flora, and larger proportions are of temperate (18.3%) and montane (11.4%) affinities. This suggests that the regions in this study tend to have boreal and cosmopolitan species in common, while temperate and montane species tend to vary among regions. This trend is supported by the fact that the largest proportion of species restricted to just one park in this study were of temperate affinity (37%), followed by species of boreal affinity (32%). Thus 47% of the temperate species, 29% of the montane species, and 14% of the boreal species in this study were restricted to just one region.

The proportion of temperate species in each flora generally fell from 17.9% in Glacier to 7.2% in Willmore, although the temperate fraction was higher in Jasper than it was in Banff. Conversely, arctic-alpine species comprise just 6.4% and 7.2% of the floras of Glacier and Waterton respectively, but make up 14.2% to 16.2% of the flora of regions to the north. Percent representation by cosmopolitan, boreal, and montane species was not related to latitude.

2.4.2 *Distributional continuity*

Percent representation by continuously-distributed species varied little between regions in this study, ranging from 49% in Waterton and Glacier to 53.6% in Willmore (Figure 2.3). Bryophytes with disjunct or interrupted distributions account for 22.1% of Waterton bryophytes. This value is comparable for other regions in this study, ranging from 18% in Banff to 23.7% in West Slopes. Twenty-eight Waterton moss species (9.7%), including *Atrichum selwynii,Brachythecium frigidum, Brachythecium hylotapetum, Claopodium bolanderi, Heterocladium procurrens, Polytrichum lyallii,* and *Tortula papillosissima* , are endemic to western North America. Forty-three such species are reported for the entire study area. Temperate species comprise 42% of western North American endemics in this study, while montane species make up 37%.

In all regions, species with continuous distributions constituted the largest proportion of species, followed by species with disjunct distributions, and finally by endemic species. This pattern was also true for the combined flora of all six regions. On the east slopes, the proportion of western North American endemic species (and endemic species in general) decreases as one moves north from 10.0% in Glacier National Park to 3.1% in Willmore (Figure 2.3). Species with continuous and disjunct distributions did not show consistent change with latitude.

2.4.3 *Morphological affinities*

The moss flora of Waterton is 36.3% pleurocarpous. The floras of all regions combined and individually were dominated by acrocarpous species (Figure 2.4). Pleurocarpous species had the greatest representation in Glacier (36.1) and Waterton. Jasper and Banff featured the lowest representation by pleurocarpous species (29.9% and 31.6% respectively) and most closely reflected the pleurocarpous proportion of the flora for all six regions (31.5%). Representation by pleurocarpous species decreased more dramatically with latitude among species exclusive to one park, falling from 38% in the unique component of the Glacier flora to 20% in Jasper and Willmore (Figure 2.4). Percent representation by pleurocarps was also low in the flora unique to West Slopes.

2.4.4 *Floristic similarity to other regional floras*

Jaccard and Sorenson similarity analyses showed that each east slopes region was generally most similar to adjacent regions (Figure 2.5), although Banff was more similar to Willmore than to Waterton, and Willmore was more similar to Banff than to Jasper (Figure 2.5). Monte Carlo simulations revealed that most similarities among east-slopes floras were greater than would be expected among random floras generated from the same pool of species. Glacier and Jasper were less similar than expected. Neither the similarity between Glacier and Willmore nor that between Waterton and Jasper differed significantly from that between randomly-generated floras.

The West Slopes flora was most similar to the floras of Glacier and Jasper (Figure 2.6), and these similarities were significantly greater than expected for pairs of random floras. Similarities between the West Slopes and other floras did not differ significantly from those expected in randomly-generated floras.

Correspondence analysis of the regional floras generally supported the affinities described above. An ordination of the six regions (Figure 2.7) shows regional floristic similarities that are closely aligned with geography, with the regions of the eastern rockies latitudinally arranged (Jasper and Willmore are reversed) along the x-axis, and the West Slopes separated from all regions of the eastern Rockies along the y-axis.

There are some species exclusive to Waterton in combination with each other region in this study (Table 2.3), but Waterton shares the most species (15) exclusively with Glacier - more than twice as many species as Waterton shares exclusively with any other park in this study (Table 2.3). These include: *Barbula unguiculata, Brachythecium asperrimum, Brachythecium holzingeri, Bryum muehlenbeckii, Dichodontium olympicum, Fontinalis antipyretica,Grimmia anomala, Grimmia dupretii, Grimmia ovalis, Homalothecium nevadense, Hypnum subimponens, Orthotrichum pumilum, Thamnobryum neckeroides, Tortula subulata,*and *Weissia controversa* . Ten species were found in all three of Glacier, Waterton, and West Slopes but nowhere else in the study area: *Bartramia pomiformis, Brachythecium erythrorrhizon, Bryum cyclophyllum, Claopodium bolanderi, Dicranum pallidisetum, Dicranum tauricum, Dryptodon patens, Heterocladium procurrens, Plagiomnium insigne,* and *Plagiothecium cavifolium*. Only three species were found exclusively in the West Slopes and in Waterton: *Pohlia atropurpurea, Racomitrium*

elongatum, and *Sphagnum riparium* (Table 2.3). Eighteen species, all but one of which were of boreal or arctic-alpine affinity, were present in all east slope regions north of Waterton and absent from Waterton-Glacier. Disjunction from Glacier to all northern regions (skipping Waterton) occurred in ten species, all of which are of boreal or arctic-alpine affinity: *Calliergon trifarium, Cynodontium strumiferum, Dicranella grevilleana, Dicranum elongatum, Dicranum fragilifolium, Meesia uliginosa, Myurella tenerrima, Paludella squarrosa, Sphagnum fuscum* and *Tayloria lingulata*.

Waterton has 14 unique species (4.8%) (Table 2.3): *Barbula eustegia, Brachythecium fendleri, Dicranum sulcatum, Lescuraea saxicola, Tortula papillosissima* (montane in global distribution), *Bryum miniatum, Buxbaumia viridis, Orthotrichum pulchellum, Tortula caninervis* (temperate in global distribution), *Brachythecium mildeanum, Warnstorfia pseudostraminea, Philonotis yezoana* (boreal), *Pohlia bolanderi* (arctic/circumpolar), and *Tortula bartramii* (global distribution unknown). Thirteen of these are rare or "S1" (known from one to five regions in Alberta - Natural Heritage Information Centre designation) species in Alberta.

One hundred and eleven of the 489 species making up the combined flora of the six regions in this study were restricted to just one region. Of these, 66 (58%) were ANHIC-tracked, accounting for 27% of the total ANHIC tracked species in the study. A further 32 (29%) of the species restricted to one region do not occur in Alberta (and thus could not be tracked), leaving only 13 species restricted to one park that would not be considered rare in Alberta. Jasper had the most species exclusive to its flora (36, or 10.5% of its flora), and Willmore had the fewest (5, or 2.2%).

2.4.5 Rare species

Waterton is home to 44% of Alberta's 282 ANHIC-tracked moss species. S1 species comprise 17.5% of Waterton mosses. Jasper is home to the most ANHIC-tracked species (164 or 58% of the ANHIC-tracked species). The fewest ANHIC-tracked species are found in Willmore (65 or 29%). The combined flora of all six regions includes 242 of these species.

Of the tracked species in this study, 26.9% were pleurocarpous. In individual regions, pleurocarps accounted for 32.5% (Waterton) to 22.6% (Jasper) of tracked species. The largest proportion of tracked

species of the combined flora of all six regions and for each of the six regions were of boreal affinity (Figure 2.8). In the south, the next greatest proportion of the tracked flora was temperate while in the west and north it was montane. The percentage of tracked arctic-alpine species is low in the south (2.9% in Glacier, and 6.5 in Waterton) and high in the north (15.9% in Jasper, 20% in Willmore). Most tracked species were continuous in distribution. Percent representation by disjunct and endemic species was greater in tracked species than in the full dataset, and representation by continously distributed species was relatively less. Endemic species accounted for 21% of tracked species in Glacier and Waterton, and 9-11% in parks further north.

2.5 Discussion

2.5.1 The moss flora of Waterton Lakes National Park

2.5.1.1 Species richness

The floristic trends and affinities shown in this study must be interpreted with reference to the limitations of the sampling approach. For example, the regional floras reported here reflect different sampling efforts. More concentrated collection will reveal the presence of species such as *Andreaea rupestris, Bryum caespiticium*, and *Hypnum cupressiforme* in Willmore, *Bryum argenteum* and *Drepanocladus aduncus* in West Slopes and *Helodium blandowii* in Banff which have likely been overlooked. Miller (1986) reports that richness of rare and endangered vascular plant species is strongly related to collecting intensity in the Appalachians, a factor that may explain the high relative representation of tracked species in Jasper. The floristic richness (be it derived of extra sampling effort, larger size or high species density) of Jasper probably also accounts for the high degree of similarity between it and the Waterton flora, and to the large number of species found exclusively in Waterton and Jasper.

The study areas are also of different sizes. Sampling area is closely related to species richness (e.g. Arrhenius 1921; Miller 1986; Palmer & White 1994), leading to a potential bias, in this study, toward greater species richness in areas of greater size. Larger areas generally posess a greater potential to encompass unique habitats or high habitat diversity. Richness of moss species has been positively correlated with microhabitat diversity (e.g. Jalonen et al. 1998; McCune & Lesica 1992; McCune et al.

1997; Newmaster et al. 2000; Vitt et al. 1995) and habitat diversity (Vitt & Belland 1997, others), due to the relatively narrow habitat preferences of many species. Habitat diversity of the Rocky Mountains probably accounts for the fact that 87% of the province's moss species were detected in the Alberta Rockies in this study, and that the combined richness of the area studied (489) approximated that of the province of Alberta (499).

The fine-scale of habitat heterogeneity of mountain ecosystems, however, should help to ensure that any region greater than a certain size will encompass a similar range of habitat conditions. The Waterton flora is comparable in number to those of much larger Rocky Mountain regions, and probably owes its relative richness largely to this phenomenon. The high specificity of mosses for habitat conditions also implies that the presence or absence of just one localized example of one unique habitat or microhabitat type (not dependent on park size) could significantly augment the regional moss flora. This study shows that in certain cases park richness has more to do with *what* habitats are present than with the park's areal extent, and that meaningful comparisons may be drawn among regions of varying sizes if the relative scale of habitat heterogeneity is consistently fine.

The placement and boundaries of parks, which reflect political rather than ecological agendas, can determine the presence or absence of unique habitats. The extreme subtlety of Waterton's foothills zone in combination with the position of Waterton's eastern boundary, for example, leads to the inclusion of well-developed prairie and parkland habitats, the presence of which are cited as a source of vascular plant diversity not present in other Canadian mountain parks (Kuijt 1973). The investigation of floristic patterns has been successfully accomplished, it should be noted, using the floras of political units of varying area (Belland 1989; McLaughlin 1986; Rice & Belland 1982).

2.5.1.2 Rare species

Vitt and Belland (1997) suggest that two centres of high species richness (13-24 S1 species/0.5^{o}x1.0^{o} grid square) exist in Alberta's Rockies: one in the Willmore/Jasper region, and another near Banff. The Waterton region is reported by Vitt and Belland to have a relatively lower concentration of rare species. They attribute this pattern to the northern affinity of arctic/alpine and boreal species, which

compose the largest proportion of rare species in the Jasper and Banff regions, and suggest that a paucity of rare temperate species in Alberta leads to low rare species richness in Waterton. In this study, nine S1 species were added to the Alberta flora in Waterton, six of which have a temperate affinity. Thus, not only does a large concentration of rare species exist in Waterton, but also the number of temperate rare species in the province is larger than first thought. That Waterton represents a significant reservoir of diversity and rare species on par with other mountain parks also underscores the necessity of viewing inventory data as dynamic – new information will be collected from under-explored regions and fields of study, and management decision-makers should be prepared for shifts in species lists.

Vitt and Belland (1997) also characterized the rare (S1) flora of Alberta according to several criteria (morphological, distributional, and climatic affinities) examined in the current study, and drew comparisons with the non-rare flora. Because the majority of species in their study occur in Alberta's mountain parks, many of their findings are similar to those revealed here. Vitt and Belland's characterization approach, however, differs from the current one in several ways. Firstly, provincially rare species in the current study are defined as having up to twenty provincial occurrences (S1 and S2 species), accounting for about 50% of the species in the study, as opposed to 25% in Vitt and Belland (1997). Furthermore, the current study compares the rare fraction of the flora to that of the complete flora for the same area, and not only with the non-rare component. These changes are expected to make the identification of trends in the rare vs. non-rare floras more conservative than that of Vitt and Belland. Vitt and Belland (1997), moreover, characterized rare species as a whole, and did not compare regions with respect to the affinities of their rare species, an aspect of the current study which sheds considerable light on the distribution of conservation value in Alberta. For example, that relatively more rare species in Waterton and Glacier are pleurocarpous, of montane affinity, and endemic and that fewer rare species are of arctic-alpine affinity compared with rare species in Banff and Jasper demonstrates patterns in the nature of rare species in different regions of the province, facilitating the interpretation and prediction of rare species distribution.

2.5.1.3 Distinctive species

The flora of Waterton is set apart from adjacent floras by the species that occur exclusively within its boundaries, and by the species that are conspicuously absent. As the fourteen species that were exclusive to Waterton did not share specific climatic, distributional, or morphological affinities, it is difficult to gather what park features, if any, allow these particular species to occupy this region. The ten species that occurred in all east-slopes parks except for Waterton were all of boreal or arctic-alpine affinity. This, along with other evidence presented in this study, may indicate that Waterton may be poor in habitats suitable for arctic/alpine species. The maximum elevation in Waterton does not meet that in other parks (Table 2.1) and Waterton has no glaciers. Lopoukhine (1970) speculates that the heavy snow cover in Waterton may hinder the spread of vegetation, and this may preferentially affect alpine species. Deep snow may also protect high-elevation substrates, making them less characteristic of alpine environments.

2.5.2 Phytogeographical affinities and distinctions of the Waterton moss flora

The moss flora of Waterton Lakes National Park is in many ways typical of all other stations in this study and of the northern Rockies as a whole. Waterton is dominated by boreal species, with other climatic affinities comprising much less of the flora. Relative representation by different climatic affinities closely corresponds to patterns in the combined flora for all six regions, and a comparable, high percentage of disjunct and widespread species is found throughout the study area. In all regions in this study, acrocarpous mosses outnumber pleurocarpous ones. A fairly consistent flora is expected: all stations in this study share similar cool, continental climates modified by similar topographic and elevational variation and similar calcareous geological formations. All regions were drastically affected by Pleistocene glaciations, and the north-south orientation of the Rockies that provided a corridor for species migration as the ice receded continues to maintain a path for migration among suitable mountain habitats. Within this broad general framework, Waterton posesses unique floristic characters which ally it closely with Glacier, making Waterton unique in the Canadian and Alberta jurisdictions in which it occurs.

2.5.2.1 Shared species affinities

Temperate, montane, and arctic-alpine species are more likely to account for differences between Rocky Mountain floras than are boreal and cosmopolitan species. Boreal and cosmopolitan habitat is continuous and abundant throughout the study area, but temperate, montane, and arctic-alpine habitats are isolated and furthermore are likely to be found at different concentrations at different latitudes and longitudes. Less floristic continuity is expected among isolated pockets of suitable habitat, both within and between climatic affinities, then among spatially-connected habitats. These types of species are thus paramount in determining the distinct character of the flora of a Rocky Mountain region.

The relatively larger proportion of species with temperate distributions in Waterton and Glacier (and the relatively smaller proportion of arctic-alpine species) compared with other regions demonstrates the effect of the more temperate climates of these parks. Maritime influence on the climate of Waterton by the 49th parallel storm track (Hansen 1948; Ogilvie 1962; Lopoukhine 1970) produces greater annual precipitation, more amplitude in seasonal precipitation, and warmer temperatures than areas to the north (Ogilvie 1962). Glacier National Park straddles the continental divide, and thus includes some temperate west slopes in its boundaries. The more northerly West Slopes flora in this study featured fewer temperate species than Waterton and Glacier, indicating, perhaps, that southerly latitude is also important for these parks.

The 49th parallel storm track and strong local winds characteristic of Waterton Lakes National Park could also create a high concentration of propagules immigrating from the west, where temperate species are more common. This phenomenon may be more important for vascular plants than for bryophytes, as light-weight spores are more readily dispersed than (heavier) seeds. Soils west of the Divide and in the path of the storm track may be protected from frost and freezing by extra snow cover, creating an environment more conducive to the persistence of temperate plants.

Western North American endemic species in this study showed a consistent decrease with increasing latitude, peaking in Waterton and Glacier (Figure 2.3). This trend is probably related to the fact that many western North American endemic species are of temperate and montane affinity.

The distributions of many of Waterton and Glacier disjunct and endemic species have distributions

centred to the south (e.g. *Brachythecium hylotapetum* (Higinbotham & Higinbotham 1958), *Bryum calobryoides* (Spence 1986), *Coscinodon calyptratus* (Muñoz 1998), *Homalothecium nevadense* (Hofmann 1998)). Schofield (1969) reports that the highest concentration of endemics occurs in areas that are environmentally diverse and that have escaped Pleistocene glaciations. The primary unglaciated areas critical for the revegetation of the northern Rocky Mountain landscape were large areas of Yukon/Alaska, the west Coast and regions to the south and east (Cannings & Cannings 1999), which remained ice-free throughout the Pleistocene. Waterton and Glacier are close to the southern limit of both Pleistocene ice sheets, and would have been readily available for colonization by species spreading north after glacial recession.

There are also several regions in this study area that may have acted as smaller, more isolated refugia. Conditions for growth on these "nunatak" refugia would have been very harsh, but bryophytes are among the most likely candidates for survival under these conditions. The Rocky Mountains mark the meeting place for the Laurentian ice sheet, which covered most north America and approached from the east, and the Cordilleran ice sheet, which originated west of the continental divide. Ice-free areas are suspected in Waterton (e.g. Rutter 1980), and refugia have also been proposed on the Porcupine Hills south to the Crowsnest Valley (Calder & Savile 1960; Ogilvie 1962; Bird & Marsh 1972). Calder and Savile (1960) note the existence of refugia for *Saxifraga lyallii* on the east slopes of the Montana Rockies, and a 1968 glacial map of Canada indicates unglaciated areas in southwest Alberta. However, evidence exists for unglaciated islands throughout the present study area, and an ice-free corridor persisted east of Rockies for most of the most recent ice age, which likely extended almost the length of the regions investigated in this study (e.g. Packer & Vitt 1974; Rutter 1980; Strong 1999).

The geographic range of vascular species unique to Waterton-Glacier is also mirrored in Waterton mosses. Of "Waterton limited" vascular plant species, many are Cordilleran in their gross distribution (Ogilvie 1962), and are more common in interior British Columbia (Kuijt 1982). Waterton often represents the easternmost Canadian locale for these, although U.S. occurrences frequently exist further east. Although the Waterton moss flora was not more similar to the West Slopes than it was to most other east-slopes regions in the current study, it includes several western species. *Claopodium bolanderi, Grimmia*

anomala, Heterocladium procurrens, and *Plagiomnium insigne* are disjunct from the coastal rain forest (Vitt unpublished). Species such as *Aulacomnium androgynum, Brachythecium erythrorhizon, Heterocladium dimorphum, Homalothecium aeneum, Polytrichum lyallii, Rhacomitrium canescens, Rhizomnium nudum,* and *Scouleria aquatica* appear more continuously from the Coast (Vitt unpublished) (Figure 2.4). Some western species, such as *Roellia roellii, Rhytidiopsis robusta*, and *Brachythecium hylotapetum* tend to co-occur (Vitt 1993), as they do in Waterton.

Affinities shared by West Slopes and eastern Rockies floras in this study may have been confounded by the broad latitudinal range of the West Slopes region. The West Slopes flora was expected to feature a greater proportion of temperate and western North American endemic species than east-slopes floras due to the relatively maritime conditions prevailing west of the continental divide. Instead, many values for the West Slopes were intermediate between those of the southern two and northern three east-slopes regions in this study.

Pleurocarpous species accounted for a slightly higher proportion of regional floras in Waterton and Glacier than in Banff and Jasper. Relative representation by pleurocarps was even greater among the rare species of southern stations. The position of the moss sporophyte helps to determine gametophytic growth form and life strategy. The abundance of strategy types in any flora is related to environmental conditions. Pleurocarpous mosses are associated with 'perennial' life strategies described by During (1979, 1992), requiring stable substrates and frequent, persistent moisture. In a study of post fire succession in Mediterranean forests (Esposito et al. 1999), pleurocarpous mosses only dominated in older stands. The often prostrate growth of pleurocarps enhances their competitive ability (Warming 1884 in During 1979, During 1992). In contrast, acrocarpous species (colonist, fugitive, and shuttle strategies – stress tolerators) tend to form cusion and turf colonies, which are generally more tolerant of or resistent to dessication and solar radiation than the loose, trailing colonies formed by many pleurocarpous species (Schofield 1985). The slightly more hospitable climate of the southern part of this study area in combination with a lower overall disturbance interval may necessitate a small shift in emphasis among resident mosses toward a more competitive strategy.

2.5.2.2 Shared species

In this study, the moss flora of Waterton is also allied with that of Glacier National Park in terms of overall floristic similarity. Rare species contribute to the distinguishing character of a flora, whereas species of intermediate abundance account for patterns of similarity (Nekola & White 1999). Although Waterton shared the greatest number of species with Jasper, Waterton and Glacier shared a significant proportion of their floras, as well as a relatively large number of exclusive species, and relatively few species distinguished them from each other. Numerical analyses confirmed the floristic affinity of the two southern regions in this study.

That the flora of each east slopes region was generally most similar (Jaccard similarily co-efficients) to adjacent regions demonstrates well-known spatial autocorrelation (Palmer & White 1994) and distance-decay relationships (Nekola & White 1999). Floristic similarity is said to be affected by environmental similarity and spatial habitat configuration (including the size and isolation of habitats and the nature of the intervening matrix), as well as by the scale of sampling and the nature of the organisms sampled (Nekola & White 1999). In the current study, patterns of (dis)similarity emerged despite the facts that distance decay in bryophytes has been shown to be less than in vascular plants (Nekola & White 1999) and that the geographical distance between floras in this study is muddied by the large size and contiguous boundaries of parks. The presence of large-scale climatic gradients and historical factors likely account for patterns seen on the scale of this study (Nekola & White 1999). Southern stations (Glacier and Waterton) which showed similarity in several respects may be floristically distinct from parks to the north: the Jasper flora was significantly disimilar to the flora of Glacier and was not significantly more similar than expected in random floras to the flora of Waterton. Increased sampling in Willmore may strengthen the differentiation between northern and southern floras. Undersampling in Banff and Willmore may have led to their apparent high similarity compared with that of Banff and Jasper.

The West Slopes were similar only to Glacier, which is partly on the west slope, and to Jasper. Again, this is surprising since Waterton is often said to have a floristic character reminiscent of regions west of the continental divide.

2.5.1 Parallel patterns in vascular and non-vascular floras

One would expect the same physical and historical factors that produced patterns of vascular plant distribution in the Rockies, including the unique flora of Waterton, to have influenced the moss floras as well. Patterns in bryophyte and vascular plant floras do not always coincide. Attempts to link patterns of vascular plant species composition to that of bryophytes have often resulted in weak or undetectable relationships (e.g. Bradfield & Scagel 1984; McCune & Antos 1981; Pharo et al. 1999; Zamfir et al. 1984). Pharo et al. (1999) point out biological differences between vascular plants and bryophytes as a source for discrepancies in their distributional patterns. The physiology of mosses makes them much more resilient to extreme or widely-varying temperature and moisture (Schofield 1985), and their small stature allows them to occupy sheltered microhabitats that may be less susceptible to climatic fluctuation. Scale of sampling is expected to affect the degree of assocation between vegetation strata, with increasing co-incidence at larger scales (McCune & Antos 1981). Despite the large scale of the current study, however, peculiarities of spore dispersal and bryophyte ecology may lead to different patterns of floristic character for non-vascular plants.

The high bryophyte richness of Waterton approximates that of vascular plants in the provincial context. Habitat heterogeneity and temperate climate probably contribute to this richness for both vascular and non-vascular plants. Furthermore, a lower frequency of disturbance by fire in Waterton compared with stations to the north may encourage the development of older stands, which are associated with high species richness and numbers of rare species (e.g. Crites & Dale 1998; Rambo & Muir 1998). Comparisons of vascular plant richness for the five regions under investigation were beyond the scope of this study, and may have revealed discrepancies undetected here. Dirkse and Martakis (1998) found that patterns of vascular and non-vascular plant species richness did not co-incide in Dutch forests.

The distribution patterns of vascular plants in the northern Rockies have been repeatedly described in terms of floristic boundaries or 'botanical watersheds'. One proposed boundary occurs at the 50° parallel (Habeck 1987; Kuijt 1982; Ogilvie 1962), leading to marked similarity between Waterton-Glacier and between the northernmost regions, but disproportionate differences between the two groups. The other corresponds to Waterton itself ('Waterton gap'), leading to coincident distributional gaps in species whose distributions continue far north and south or east and west of the park. The existence of floristic boundaries

is controversial, and most attempts to find them conclude that floras change gradually over space and cannot be clearly delimited (e.g. Belland 1989; McLaughlin 1986; Thaler & Plowright 1973). The detection of a "watershed" between Waterton and Banff is made likely by the presence of a geographical gap among otherwise contiguous parks. In fact, if collections of vascular plants follow patterns of concentration similar to those of moss collections (i.e. in mountain parks), lack of data may account for the boundary originally reported for that area of the Rockies. With few exceptions, such as the continental divide, natural and political boundaries do not coincide. Therefore, it would be surprising to discover natural floristic boundaries (Belland 1989) by comparing park floras.

In the moss floras examined in this investigation, evidence of a floristic boundary between Waterton and Banff is weak. Similarity indices show dissimilarity between Waterton/Glacier and Jasper. Evidence for a floristic boundary between Waterton and Banff should include, instead, disimilarity between them. However, many species are found in all eastern Rockies regions in this study except Glacier and/or Waterton, and Waterton and Glacier shared relatively many species exclusively, compared with Waterton and other regions. Waterton and Glacier National Parks show marked similarity in the climatic affinities and distributions of their moss species (e.g. high proportion of temperate and endemic species), as do Banff, Jasper, and Willmore, but pairs of regions from each group show largely different patterns. These factors seem to indicate floristic integrity within the northern and southern regions in this study. The widest gap between two eastern regions in the Correspondence Analysis ordination occurred between Waterton and Banff (Figure 2.7).

The 'Waterton gap' noted in the distributions of vascular plants may to some extent be seen in the ten boreal and artic-alpine mosses known for all east Rockies regions except Waterton. Vascular plant species inexplicably rare or absent from Waterton, including *Empetrum nigritum, Tofieldia glutinosa*, and *Cornus canadensis* (Kuijt 1982) are also boreal and northern species. It should be noted that several of the species used as evidence for a Waterton gap have since been found in greater abundance within Park boundaries.

2.6 Conclusions

The climate, elevation, and glacial history characteristic of Glacier, Waterton, Banff, Jasper, Willmore, and West Slopes, superimposed on the broadly consistent physical and floristic character of these regions, produces a continuum of floristic change in the mosses of the northern Rockies. In this continuum, Waterton Lakes National Park features more temperate and western North American endemic species than regions to the north. Despite differences in park size, the regions are remarkably similar in known richness, and Waterton supports a large proportion of rare species compared to nearby regions of far greater area.

The localized concentration of western species and the conspicuous absence of arctic-alpine species present in neighbouring regions, as observed in the Waterton vascular plant flora, are seen at least to some extent in the moss flora. It seems likely that similar climatic or historical events contributed species of both types to the landscape. The floristic boundary at 50° latitude described for Rocky Mountain vascular plants is not clearly present in the moss flora, although the moss flora of Waterton is generally far more similar to that of Glacier, to the south, than to regions further north.

Further field and herbarium studies will contribute reliability to species lists for the regions in this study. Sampling between Waterton and Banff must be conducted, and herbarium records for this region should be assembled.

2.7 Management recommendations

The identification of features contributing to the conservation value of a park allows for the protection of these features and aids the establishment of management priorities. Managers of Waterton Lakes National Park are advised that the significance of the Waterton moss flora lies in:

a) The presence of particular species. Fourteen species occurred only in Waterton in this study, and several more were found only in Waterton and Glacier or in Waterton and West Slopes. Preserving these species will contribute to the preservation of the Canadian and Alberta floras.

b) The presence of provincially rare species. These 124 species are known from fewer than 20

locations in the province and their persistence in the Alberta flora depends on their protection.

c) High representation by western North American endemics and temperate species. The existence of these species indicates the presence of unique climatic and/or historical factors in the park. These species may indicate the presence of unique habitat for other organisms as well.

d) The presence of many moss species. Despite its small area, the moss flora of Waterton rivals that of much larger parks which have been explored in greater depth. Climatic, physical, and historical factors created and maintain this richness. It is an important reservoir for diversity in Alberta. Species lists are dynamic and will evolve with time.

2.8 Literature cited

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Table 2.1. A comparison of key physical characters and moss floras of the study areas examined in this investigation. East slopes regions are listed from south (left) to north (right); West Slopes occurs exclusively west of the continental divide.

	Glacier	Waterton	Banff	Jasper	Willmore	West Slopes
Area (km^2)	1349	540	6641	10 878	4597 (area of Willmore Wilderness)	**Kootenay**: 1406 **Yoho**: 1310
Elevational Range (m)	948 – 3190	1280 - 2940	1338-3628	985 – 3782	975 – 3098	**Kootenay**: 818 – 3424 **Yoho**: 1300 - 3562
Position with respect to continental divide	East and west	East	East	East	East	West
Known moss flora (# of spp.)	280	288	271	344	226	285

Table 2.2. List of the habitat types of Waterton Lakes National Park, compiled with reference to literature Kuchar 1973, Lopoukhine 1970) and field reconnaissance. It was intended that by sampling several examples of each type, the full moss diversity of Waterton Lakes National Park would most accurately be captured.

Habitat type	Definition
Coniferous forest	Overstory consists purely of coniferous trees
Deciduous forest	Overstory consists purely of deciduous trees
Mixedwood forest	Overstory consists deciduous and coniferous trees in a ratio of at least 25%:75% (or vice-versa)
Talus	Sloping rocky debris at the base of a cliff or exposed high elevations
Coniferous scrub	Overstory consists of patchy coniferous trees less than 3m high
Forested cliff	Cliff is shaded by forest overstory
Unforested cliff	Cliff is unshaded by forest vegetation
Alder	Overstory consists purely of Alnus spp.; steeply-sloping
Alluvial gravel	Flat mineral substrate (sand-coarse gravel) associated with rivers or streams; much substrate exposed. Overstory vegetation is sparse
Wetland	Flat or gently-sloping, peat- or organic-substrate, saturated at least in patches
Stream	Stream course and banks. May be intermittent or continuous within the summer season
Grassland	Dominated by graminoids, no more than 10% tree cover in any 10 x 10m area
Meadow	Treeless, high-elevation, non-rocky or minerally herbaceous community

Table 2.3. Comparison of the number of species in this study that were unique to each park or region (were recorded or reported only once), and of the number of species that were shared exclusively by Waterton and one other park (or region). East slopes regions are listed from south (left) to north (right); West Slopes occurs west of the continental divide.

	Glacier	Waterton	Banff	Jasper	Willmore	West Slopes
Number of species exclusive to one park	21	14	10	36	5	27
Number of species exclusive to Waterton and one other park	15	-	5	7	2	3

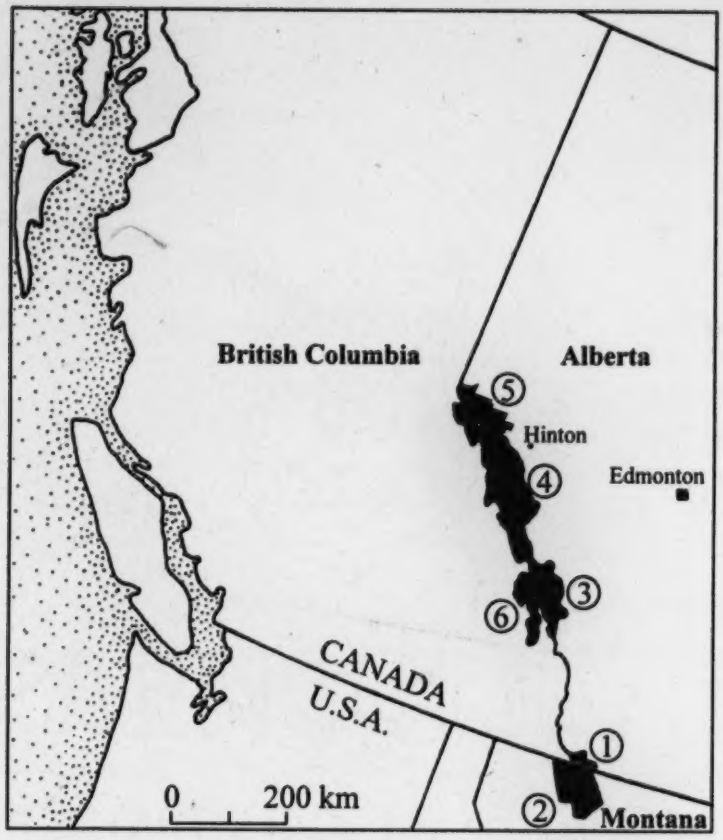

Figure 2.1. Map of the northern Rocky Mountains (northern United States and southern Canada) showing the location of Waterton Lakes National Park (1) and five other regions (Glacier National Park (2), Banff National Park (3), Jasper National Park (4), Willmore Wilderness Park (5), and Kootenay and Yoho National Parks (6)) with which the Waterton moss flora was compared. Kootenay and Yoho, together with Kinbasket Lake, which extends north of the two National Parks, comprised the area known as "West Slopes" in this study.

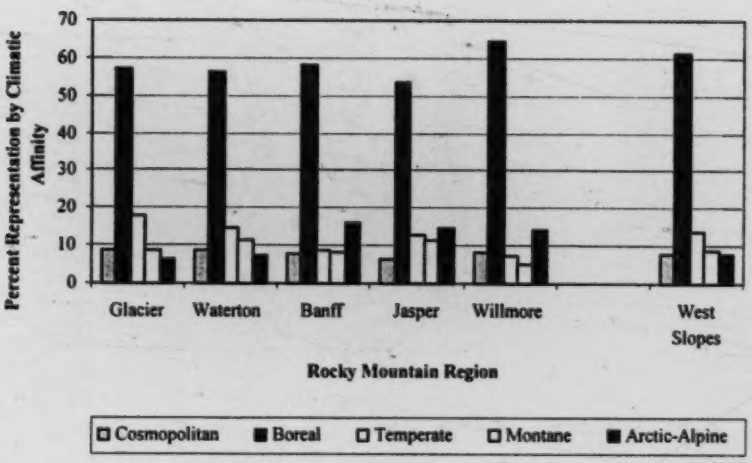

Figure 2.2. Percent representation in the moss floras of six regions of the northern Rocky Mountains by species of different climatic affinities. East slopes regions are listed south (left) to north (right). A gap separates regions on the east slope of the continental divide from that which occurs exclusively on the west slope.

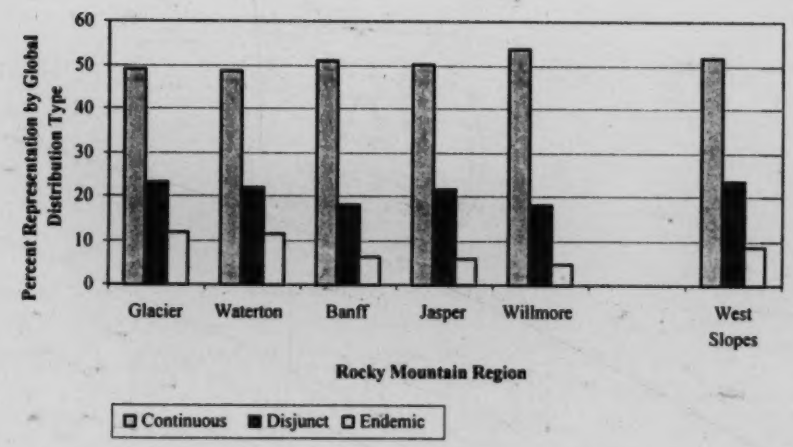

Figure 2.3. Percent representation in the moss floras of six regions of the northern Rocky Mountains by different world distributions. East slopes regions are listed south (left) to north (right). A gap separates regions on the east slope of the continental divide from that which occurs exclusively on the west slope.

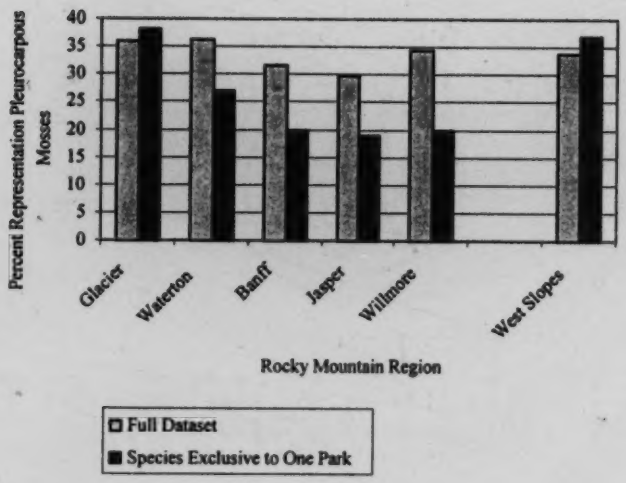

Figure 2.4. Relative representation by pleurocarpous mosses in the moss floras of six Rocky Mountain regions, and in the portion of each flora which is exclusive to that region (of the six regions). East slopes regions are listed south (left) to north (right). A gap separates regions on the east slope of the continental divide from that which occurs exclusively on the west slope.

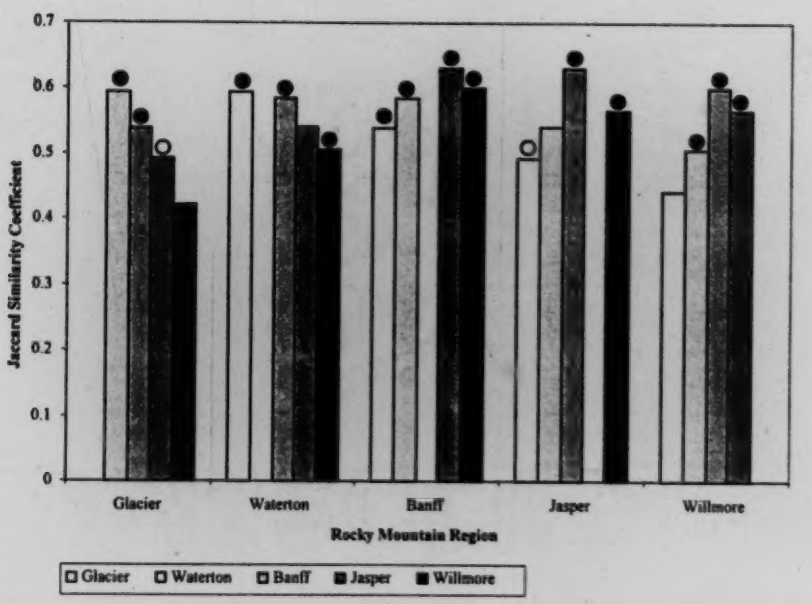

Figure 2.5. Jaccard similarity co-efficients for the moss floras of each pair of five east-slopes Rocky Mountain regions. Closed circles signify that the similarity between floras exceeded that expected in random floras containing the same pool of species (Monte Carlo simulation with thirty iterations). Open circles denote similarities that were less than expected in random floras. Similarities that did not differ significantly from expected are depicted by bars without circles.

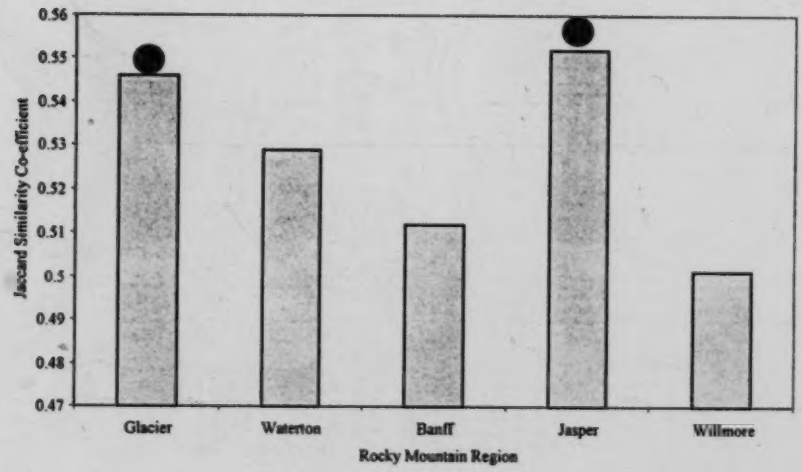

Figure 2.6. Jaccard similarity co-efficients for the moss flora of the West Slopes and each of five east-slopes Rocky Mountain regions. Circles signify that the similarity between floras exceeded that expected in random floras containing the same pool of species (Monte Carlo simulation with thirty iterations). Similarities that did not differ significantly from expected are depicted by bars without circles.

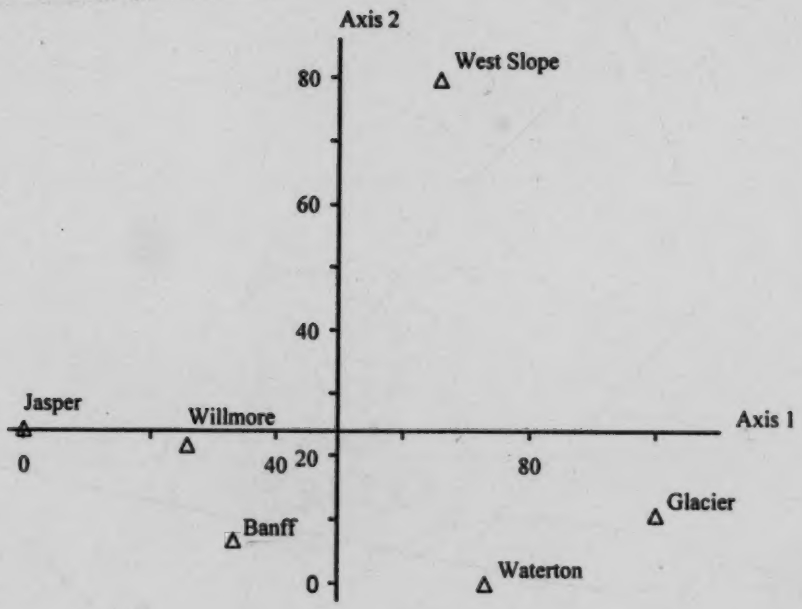

Figure 2.7. Correspondence Analysis ordination of six Rocky Mountain moss floras based on presence/absence data for 489 species. Axes 1 and 2 account for 27.7% and 23.8% of the variance in the species data respectively.

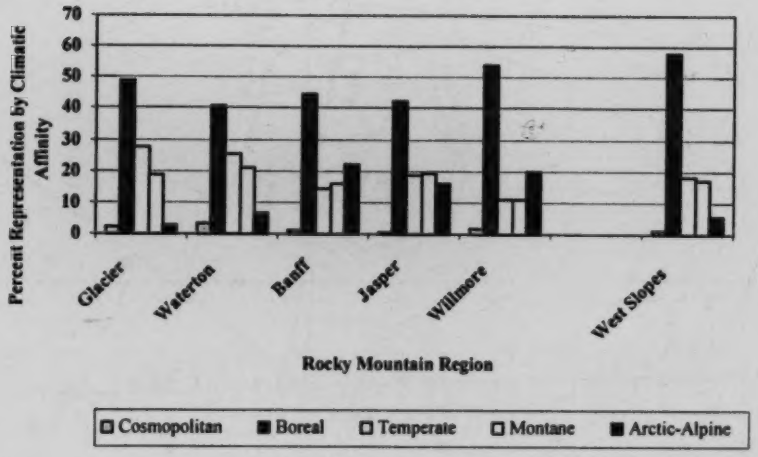

Figure 2.8. Relative representation by different climatic affinities of rare mosses (provincially rare / tracked) in the floras of six Rocky Mountain regions. East slopes regions are listed south (left) to north (right). A gap separates regions on the east slope of the continental divide from that which occurs exclusively on the west slope.

3. PATTERNS OF MOSS COMMUNITY COMPOSITION AND CONSERVATION VALUE IN WATERTON LAKES NATIONAL PARK, WITH IMPLICATIONS FOR PARK MANAGEMENT

3.1 Introduction

Many park mandates dictate the preservation of natural biodiversity while most park budgets preclude the scientific investigation required to guide informed biodiversity conservation management. Species inventories, among the most reliable methods of assessing site conservation value, can realistically only address small subsamples of the area and organisms within park boundaries. Efficient, thorough interpretation of inventory data for patterns that can be translated into practically applicable management recommendations is critical.

Bryophytes are difficult to locate and identify, traits that traditionally relegate them to the overlooked majority in species inventories (e.g. Cox & Larson 1993; Pharo & Vitt 2000). As their key roles in ecosystem function (e.g. LaRoi & Stringer 1986; Longton 1984; Økland 1994; Slack 1988; Smith 1982; Vitt 1991) gain recognition they are increasingly included, yet basic understanding of bryophyte community and conservation ecology still lags behind that of groups such as vascular plants and mammals. In addition to pinpointing key inventoried sites supporting maximum bryophyte species diversity or rarity, therefore, it may be useful to identify accessible correlates of conservation value to aid managers in making informed decisions for uninventoried land (e.g. Gould & Walker 1999; Jonsson & Esseen 1990; Kruys et al. 1999; Ohlson et al. 1997; Pharo & Vitt 2000; Rambo & Muir 1998a,b; Vitt et al. 1995).

Patterns of bryophyte conservation value have been investigated from several perspectives in recent years. Vitt and Belland (1997), for example, suggest that rare species distribution in Alberta relies on the presence of certain habitat types (cliffs and alpine habitats) that generally feature high microhabitat diversity and that are not dominant on the landscape. Moss conservation value has not been correlated with habitat types beyond this generalization, but such correlations would greatly facilitate site assessment for moss conservation on a park scale, because the identification of habitats is quick and easy.

Bryophyte communities are often excellent indicators of the habitat conditions under which they occur (Slack 1990; Vitt & Belland 1997). Whereas habitat types are generally defined by physical features and dominant vegetation, moss communities can signal intricacies of local habitat that are not immediately obvious to the casual visitor. Vitt et al. (1995) investigated bryophyte species diversity with respect to different peatland communities. The five community types they worked with are distinguished largely with respect to bryophyte species known to indicate local water chemical conditions. By analysing these communities separately, Vitt et al. (1995) were able to discover important patterns of species diversity with respect to community types and environmental gradients that were not visible when all communities were analyzed together. If certain communities are predictably more rich than others, managers may be able to direct development away from sites which are home to certain reliable community indicator species.

Patterns of bryophyte conservation value with respect to bryophyte habitat and community types imply, in turn, patterns of conservation value with respect to environmental gradients. Ordination techniques are useful ways of exploring the relationship of species composition, environment, and conservation value (e.g. Gould & Walker 1999; Lee & LaRoi 1979; Rambo & Muir 1998a). Canonical correspondence analysis (ter Braak 1987), for example, can help to identify key environmental variables explaining variation in species composition at sites of conservation interest. In turn, community classifications or quantitative measures of conservation value may be correlated with ordination axes. The relative positions and spatial fidelity of these conservation values on ordination diagrams reveals relationships of species composition, environment, and conservation value.

Many criteria define conservation value, the most common of which include species richness and rarity (e.g. Margules & Usher 1981). Species may be considered rare on local (park), provincial, national, and global scales, each of which results in the compilation of a unique tracking list. Locally rare species make up a large proportion of local diversity (e.g. Vitt 1991; Vitt & Belland 1995, 1997), the maintenance of which is often a key goal for protected areas. Provincially, nationally, and globally rare species depend on protected areas for their persistence on a larger scale, and as parks are often managed or supported by provincial or national governments, it is their mandate to protect threatened species. Aspects of richness and different scales of rarity are rarely considered in a single project (but see White & Miller 1988). It is important to recognize patterns of several different kinds of conservation value so that the park management

may apply recommendations that most closely reflect their priorities.

Patterns of moss species composition, richness, and rarity are often investigated within a single habitat type (e.g. Cox & Larson 1993; Glime & Vitt 1987; Gould & Walker 1999; Jonsson 1996; LaRoi & Stringer 1976; Pharo & Vitt 2000; Vitt et al. 1995). Investigation of all representative habitats within a park jurisdiction is far less common, though perhaps more applicable to park management (Heikkinen 1998).

The objectives of this investigation are

1) to pinpoint 'hotspots' of high moss conservation value in Waterton Lakes National Park
2) to determine patterns of moss conservation value with respect to moss habitats and communities
3) to explore the relationship between gradients of site conservation value, species composition, and local environment
4) to interpret patterns of moss conservation value in a management context.

3.2 Study area

Waterton Lakes National Park (Waterton), a relatively small (530 km^2) mountain park in the extreme south-west corner of Alberta, Canada (Figure 3.1), was established in 1895. It is bounded in the west by the British Columbia border, which coincides with the continental divide. The southern park boundary is the Canada-United States border, across which Waterton is contiguous with its American counterpart, Glacier National Park. A unique combination of interacting climatic, physiographic, geologic, and historical factors contributes to the rich and unique flora, complex vegetation, and diversity of habitats found within the park, and may influence the distribution of moss conservation value there.

3.2.1 Physiography

High mountains and deep valleys are found in Waterton (Breitung 1957; Kuijt 1982). Elevation ranges from 1254 to 2715 m above sea level (Lopoukhine 1970). The low relief of the foothills zone at this point in the Rocky Mountains leads to the presence of rolling prairie in the east part of the park.

3.2.2 Climate

Within Waterton, as in all mountainous areas, climate varies markedly in tandem with elevation. Insolation intensity, ultra-violet radiation, cloud cover, and precipitation generally increase with elevation while ambient and surface temperature and growing season length decrease (Daubenmire 1943; Poloquin 1973; Tivy 1993). Windspeed is lowest midslope and increases toward elevational extremes (Daubenmire 1943). A higher snow:rain ratio and longer snow persistence also accompany increases in elevation (Breitung 1957; Lopoukhine 1970). Slope, aspect, and topography modify elevational climate trends (Daubenmire 1943). Tivy (1993) states that slope in relation to the direction and incidence of sun is the most critical factor determining local climate and vegetation, because of its overriding effect on light and temperature conditions. Moisture, air circulation, growing season, and frost conditions can all be traced to these factors. Furthermore, west-facing slopes in Waterton, particularly those near the Continental Divide are most affected by the maritime influence of moisture-laden prevailing west winds (Daubenmire 1943; Hansen 1948; Ogilvie 1962; Lopoukhine 1970), resulting in especially high annual precipitation. Average daily minimum and maximum temperatures within Waterton are approximately 6°C and 24 °C, respectively, in July and -16 °C and -1°C in January (Finklin 1986). The 795 to 1346 mm of annual precipitation fall mostly in winter and spring (Finklin 1986, Parks Canada (pers. comm,)). Daily windspeed averages 32 km/hr, from the southwest, with gusts to 120 km/hr or more (Parks Canada (pers. comm)).

3.2.3 Vegetation / habitat types

Vegetation in Waterton conforms to the elevational zonation described by Daubenmire (1943) for the Rocky Mountains. It is most characteristic of Rocky Mountain vegetation on east-facing slopes, while the maritime influence of west winds lends more coastal character to west-facing vegetation. Waterton's vegetation may be divided into three principle types that in turn vary closely with local climate. These include two treeless zones at high and low elevation extremes with an intervening forest zone (Breitung 1957; Kuijt 1982). At low elevations, wetlands, parkland, and dry grassland predominate. Wooded vegetation is largely limited to *Populus* groves and to pure thickets of *Salix* and *Betula*. Higher up, relatively pure, even-aged stands of *Pinus contorta* precede *Picea engelmannii* and *Abies lasiocarpa*

following disturbance such as fire. All successional stages in this progression are represented within park boundaries, and at least two thirds of the mountain slopes are covered by coniferous forest (Breitung 1957). Shrub-covered avalanche slides often interrupt forest vegetation, particularly on south-facing slopes (Breitung 1957). Stunted *Pinus flexilis*, *Pinus albicaulis*, and *Abies lasiocarpa* occur above the coniferous forest, and decrease in height and density until krummholz vegetation accounts for the only tree cover. Timberline occurs at approximately 2100 m (Breitung 1957) but may be elevated locally on sheltered, concave slopes (Tivy 1993). Open herbaceous meadows at high elevations grade into alpine semidesert consisting of rocky meadows and ridges of varying stability. Exposed bedrock accounts for approximately 23% of Waterton's area (Lopoukhine 1970).

3.2.4 Flora

The extremely complex geology, steep environmental gradients, and unique, spatially varied climate of Waterton combine to foster a unique and rich vascular flora (Breitung 1957; Kuchar 1973; Kuijt 1982). Fifty-five percent of the province's vascular plant species (Kuijt 1973) including over half of Alberta's rare vascular species (Ogilvie 1962; Kuchar 1973) exist within the park - less than 0.1 % of the province's area (Kuijt 1973). Prairie, boreal, arctic-alpine, Cordilleran, endemic, cosmopolitan, and exotic vascular plant species are represented (Kuchar 1973).

The Waterton moss flora is also rich relative to the small area it occupies, probably due to a high, fine-scale habitat diversity and a more temperate climate than regions to the north (chapter 2). Temperate and western North American endemic species represent a greater proportion of the Waterton flora than of floras of Rocky Mountain parks to the north while relatively fewer arctic-alpine species occur in Waterton (chapter 2). A relatively large proportion of Waterton species (vascular and non-vascular) are Cordilleran in their gross distribution (Ogilvie 1962), and are more common in interior British Columbia (Kuijt 1982).

3.3 Methods

3.3.1 Moss collection and identification

Thirteen habitat types (Table 3.1) within Waterton Lakes National Park were identified using published accounts (Kuchar 1973; Lophoukine 1970) and field reconnaissance. Field reconnaissance began in 1996, and entailed hiking throughout the Park and noting the range of habitat conditions encountered. The working habitat classification developed in 1996 was applied the sites encountered early in the 1997 sampling season, and the classification was modified as necessary. The designation of habitat types relied on readily-discernable vegetation, substrate, and moisture characteristics (Table 3.1). At least 4 sites representative of each type (total 112 sites) were selected for sampling with reference to Ecological Land Classification vegetation maps (Achuff et al. 1997), but primarily through field reconnaissance. Because species capture was of paramount importance, maximizing park area covered and variability within habitat types were primary criteria in site selection. Accessibility and impact on park visitor experience were also considered.

In the summer of 1997, representative microhabitats within each site were systematically examined until no new moss species were found (McCune & Lesica 1992; McCune et al. 1997; Newmaster 2000). Microhabitat types (e.g. cliff ledges, boulders, rotten logs, tree bases) present in the site were noted with the aid of a checklist. Examples of each type were visited. The full extent of each example (e.g. all aspects and elevations of a tree base) were carefully searched for moss inhabitants. In the case of boundless microhabitats, such as the forest floor, several representative areas were intensively searched, and additional species encountered between bounded microhabitats were also noted. Species identification generally followed the concepts of Lawton (1971), with additional reference to Crum and Anderson (1981), Horton (1983), Koponen (1974), Peterson (1979), Shaw (1982), Spence (1988), and Syed (1972) for certain taxonomic groups. Voucher specimens are stored in the University of Alberta Cryptogamic Herbarium (ALTA).

3.3.2 Environmental variables

Environmental data were estimated at each site on a one-time basis (Table 3.2). Selection of environmental variables for measurement involved surveying environmental factors important for bryophyte

species growth, composition, and/or richness in previous studies (e.g. Alpert 1985; Belland & Vitt 1995; Frego & Carleton 1995; Glime & Vitt 1987; Hedderson & Brassard 1990; Muotka & Virtanen 1995; Newmaster 1996; Pentecost 1980; Slack 1990; Stephenson et al. 1995; Vitt et al. 1995; Yarranton 1968), and determining which factors were likely to vary on the scale of the bryophyte sampling. Methods for measuring environmental variables were selected to be quick, inexpensive, and simple and may have sometimes sacrificed accuracy in favour of these attributes (Table 3.2). For example, estimates of percent cover were made visually without the aid of physical grids or plots, and were generalized for an entire site, Capturing relative differences in environmental conditions was deemed more important than gathering absolute values. It was assumed that these relative differences persist from year to year. Two weeks of continuous field work were required to visit all sites in this study, many of which were safely accessible only after snowmelt, precluding the application and comparability of season-long collection of temperature, light, and precipitation data. Some variables were only applicable to particular habitat types, and thus were restricted to analyses involving only those types (Table 3.2).

3.3.3 Identification of moss conservation hotspots

Moss conservation hotspots were those sites with the highest richness in each of the following four categories. Coldspots were sites with the lowest richness in the same categories.

1. **Moss species richness** (site alpha diversity) was selected as an indicator of moss diversity due to its simplicity, wide acceptance (e.g. Gaston 1996; Magurran 1988) and freedom from assumptions of relative species importance.
2. **Richness of species endemic to western North America** was selected for its relevance to global biodiversity and because these species tend to be at the eastern edge of their ranges in the Rocky Mountains. Species at range limits are of particular significance to conservation because they are most susceptible to extinction and to evolutionary pressure. Fewer than 5 mosses in Alberta are known to be globally rare (designated G1 or G2 by ANHIC 1999), and none of these is known to occur within Waterton.
3. **Richness of provincially rare species** was defined as the number of species at each site that were tracked by the Alberta Natural Heritage Information Centre (ANHIC 1999) (generally 1

to 20 provincial occurrences). 'S1' species (1 to 5 provincial occurrences) were considered as a subset of provincially rare species in some analyses.

4. **Richness of locally rare species** is of significance to conservation because the global extinction of a species results from the accumulation of local extinctions. Furthermore, the majority of species in any given study area are locally rare (e.g. Vitt 1991; Vitt & Belland 1995, 1997), forming the foundation for local diversity. Species occurring in one to five sites within Waterton were designated as locally rare.

Conservation 'hotspots' and 'coldspots' were identified by mapping the sites with the 9-12 highest and lowest values among all sites for each of the above criteria.

3.3.4 Conservation value of habitats and communities

Habitat types dominating among conservation hotspots and cold-spots were recorded. In order to assess the degree to which the sampling effort devoted to each habitat type captured the variability in its moss flora, species/sampling effort curves were developed for each habitat type using PCOrd software (McCune & Mefford 1999). Mean species richness and number of provincially rare species in the 13 habitat types identified before sampling were compared using simple one-way ANOVA (SPSS). Statistical assumptions for ANOVA were not met for the number of locally rare species, the number of S1 species, or the number of western North American endemic species. The beta and gamma diversities of each habitat type were also compared. Because unequal numbers of sites were sampled for each habitat type, species/sampling effort curves were used to estimate gamma diversity (Whittaker 1972) at different levels of sampling effort. Species turnover (beta diversity) (Whittaker 1972) was calculated using these gamma diversity estimates. In this way, the beta and gamma diversities of different habitat types could be ranked despite the unequal sampling effort devoted to each type.

For further analysis, the dataset was subdivided into two groups consisting of 33 restricted habitat sites and 79 unrestricted habitat sites respectively. The terms 'restricted' and 'unrestricted' are proposed by Vitt and Belland (1997) to describe the role of different habitat types as dominant on the landscape or occupying small, clearly-defined patches within the dominant habitat matrix. According to this concept, streams and forested/unforested cliffs were defined as restricted habitats because they could be

encompassed within examples of all other habitat types in this investigation, which were, correspondingly, designated 'unrestricted'. A third site data subset (including 29 forested habitats) was created in order to simulate the more common practice of investigating patterns within a single habitat type (e.g. Cox & Larson 1993; Glime & Vitt 1986; Gould & Walker 1999; Jonsson 1996). These four site datasets – restricted, unrestricted, forested, and all sites – were compared using the methods described above, and were each investigated for patterns of species composition and conservation value through the analyses described below.

For each dataset, TWINSPAN (Hill 1979; Gauch & Whittaker 1981) analysis (using PCORD (McCune & Mefford 1999)) was implemented to identify moss community types. Very rare (fewer than 4occurrences) and very common (greater than 45 occurrences) species were withheld from the analysis because they were not considered useful in clustering sites into communities. Rare and common species cut-offs in this instance were arbitrary. Mean conservation values, beta diversity and gamma diversity of TWINSPAN community groups were compared in the same way as habitat types.

3.3.5 Patterns of conservation value with respect to compositional and environmental gradients

Canonical Correspondence Analysis (CCA) was used to relate patterns of bryophyte species composition to environmental variables (ter Braak 1987). Canonical correspondence analysis is a direct gradient analysis in which species data is structured so as to maximize the strength of its relationship, via multiple regression, to environmental data.

Canonical Correspondence Analysis is recommended for situations in which a Gaussian response of species to environment is assumed. The presence/absence data collected in this study precludes the detection of an abundance response to environmental variables. Furthermore, due to the large number of locally rare and habitat-specific species, this dataset includes a large number of zeros (fewer than 10% of the cells in the species-by-sites grid contained non-zero values). Thus, in order to extract dominant patterns, data was transformed according to Beals smoothing function (McCune 1994) to replace presence absence data with a measure of the 'favourability' of each site for each species.

PCOrd software (McCune & Mefford 1999) was used for the analysis. For each site data subset, environmental variables were log-, square-root-, or arcsin-transformed following recommendations by Zar

(1996) to more closely approximate normal frequency distributions, as suggested by Økland and Eilertsen (1994). Species with three or fewer occurrences or greater than 45 occurrences were removed from the data used to create ordinations. Variance partioning (Borcard et al. 1987; Okland & Eilertsen 1994) was used to identify individual explanatory variables that were significant in explaining variation in the full dataset and each of three site data subsets (see above). All of these variables, regardless of intercorrelation, were included in CCA ordinations. Community groups and site conservation value (richness, number of locally rare, provincially tracked, S1, and western North American endemic species) were overlaid on CCA ordination diagrams, and conservation value was correlated with ordination axes.

3.4 Results

3.4.1 Conservation hotspots

Conservation hotspots for each conservation category are mapped in Figure 3.2.A. Most sampled sites of high conservation value in all categories occur in the southwest corner of Waterton, with one concentration near Upper Waterton Lake and a second concentration occurring near the Continental Divide. Nine of the ten richest sites fell within the southwest region, as did most of the sites of high conservation value in more than one category. High provincially rare species richness and western North American endemic species richness were observed in the northwest. A small, isolated pocket of locally-rare species richness was sampled in a wetland complex in the east part of the Park. The distribution of cliffs and streams (restricted habitat types) sampled in this study (Figure 3.2B) is mostly confined to the southwest.

Conversely, sites with no western North American endemic species, no locally rare species, and no provincially rare species were distributed throughout the park (Figure 3.2.C). Sites with no species important with respect to any of the three rarity conservation criteria were restricted to the north and east. Similarly, the 18 sites with an overall richness of seven or fewer species occurred largely in the north and east, with just four sites within the southwest region.

3.4.2 Habitat correlates of moss conservation value

Conservation hotspots included six habitat types in total, and included streams and forested cliffs for all four conservation criteria (Figure 3.3A). Coniferous forests and unforested cliffs were also common.

Unforested cliffs were unrepresented in this top fraction for western North American endemics, and coniferous forest was unrepresented in the sites with the highest number of provincially and locally rare species. Wetland accounted for half of the hotspots for locally rare species and one of the top nine sites for western North American endemics. Twelve of the thirteen habitat types were represented among conservation coldspots (Figure 3.3B), including some types that were represented among conservation hotspots. Alder, coniferous scrub, deciduous forest, grassland, and talus sites were among sites that supported no globally, provincially, or locally rare species.

For all four conservation criteria, coniferous forest, forested and unforested cliff, stream, and mixedwood site types had the highest average conservation value (Table 3.3), except in the case of locally rare species, in which wetlands had the greatest average number of locally rare species and mixedwood sites were not among the top five. Alder slopes, meadows, grasslands, coniferous scrub and deciduous forests generally supported the lowest mean conservation value. Variability in mean conservation value, as indicated by standard deviation, was consistently highest in forested cliffs (Table 3.3). Significant differences between high and low mean richness and number of provincially rare species were observed (Table 3.3), and showed different patterns for richness and provincially tracked species. Restricted habitat types, as a group, have significantly greater mean conservation value than unrestricted habitat types for all conservation criteria (Table 3.3). They also feature significantly more microhabitats (greater complexity, $p<0.001$) than unrestricted mesohabitat types.

Almost every habitat type sampled in this study featured species that were not present in any other habitat type (Table 3.4). Most of these species (57 of 78) occurred just once. The number of species exclusive to wetlands and streams is much greater than the number exclusive to other habitat types (Table 3.4), and includes 8 (e.g. *Helodium blandowii, Hypnum lindbergii, Leptodictyum riparium, Sphagnum warnstorfii, Tomenthypnum nitens*) and 10 (e.g. *Brachythecium asperrimum, Bryum cyclophyllum, Hygrohypnum bestii, H. ochraceum, Pohlia proligera*) species (respectively) that occur in 2 to 8 sites. No species were exclusive to alder or mixedwood habitats. More species were generally exclusive to unrestricted habitats, as a whole, than to restricted ones, except that a greater number of provincially tracked species were exclusive to restricted habitat types.

Species/sampling effort curves for individual habitat types did not level off (Figure 3.4). High gamma diversity was projected in streams, cliffs, coniferous forests, and wetlands (Figure 3.4). There was no change in the rank of beta diversity of the habitat types from n=5 to n=17 (Figure 3.5), although the behaviour of species/sampling effort curves suggests some change in rank may occur beyond the number of sites sampled (Figure 3.4). Assuming that the rank of sites would have remained the same for all habitat types at all levels of sampling effort, coniferous scrub habitat displayed the greatest species turnover, followed by wetlands, deciduous forest, and streams. Mixedwood, coniferous forest, and forested and unforested cliffs displayed the least species turnover.

Greater gamma diversity is suggested by the species-area curve for restricted habitat types compared with that for unrestricted habitat types or forested sites (Figure 3.4). Beta diversity at the 33-site sampling effort level was 7.9 for unrestricted habitats compared with 5.6 for restricted habitat types.

Species richness and richness of rare species were significantly correlated (Table 3.5). Richness of locally rare species showed consistently low correlation with other measures of conservation value. Similar patterns of correlation were observed in the full and unrestricted datasets, while restricted habitats showed slightly different trends. Tracked species richness was not correlated with any other conservation value in forested sites.

3.4.3 Community correlates of moss conservation value

Eight communities resulted from TWINSPAN analysis of the entire species dataset (Figure 3.6.A). The initial division separated most permanently wet sites from all other sites. Streams occurring in this group proved to be permanent, in that they were flowing both at the beginning and end of the growing season, as opposed to those that dried up at least periodically during the summer. Preferential species for the two permanently wet communities (*Drepanocladus aduncus* and *Brachythecium erythrorrhizon* communities) are characteristic of stagnant (or very slow-moving) and flowing water respectively. Division of the drier sites initially separated most forested sites (indicated by *Brachythecium starkei*) from most unforested sites (indicated by *Pseudoleskeella tectorum*). *P tectorum* is characteristic of rocky substrates, whereas *B. starkei* is characteristic of forest soil floors. Two forested community types were accepted. Indicator and preferential species for the *Mnium spinulosum* community are associated with mesic, low-

elevation forests and organic substrates, whereas the *Polytrichum piliferum* community was characterized by species generally preferring an open canopy, higher elevation, and a range of mineral and soil substrates. The unforested sites were divided into four community types: A dry *Weissia controversa* community made up of species characteristic of dry, open soil; a *Brachythecium velutinum* community generally affected by forest cover and organic substrate; and two communities (*Tortula norvegica* and *Homalothecium aeneum*) characterized by a preference for mineral substrate but differentiated by their association with exposure and shade, respectively.

Separate TWINSPAN classification of restricted and unrestricted mesohabitat types also showed moisture as an initial criterion for division (Figures 3.6.B,C). In unrestricted habitats, a *D. aduncus* community (Figure 3.6B) characterized by species preferring slow or stagnant water and organic substrates was identified, and in restricted habitats, the permanently wet *Bryum weigelii* community (Figure 3.6.C) was characterized by species preferring flowing water and mineral substrates. Subsequent divisions of unrestricted mesohabitats were similar to those in the full dataset, in that mesic, forested sites were initially segregated from exposed, dry sites, and that several similar communities finally resulted. *Brachythecium hylotapetum* and *Pohlia bolanderi* communities, for example, appear to be roughly analagous to the *Mnium spinulosum* and *Weissia controversa* communities. In the restricted site datset, in contrast, only two more communities (*Homalothecium aeneum* and *Amphidium lapponicum*) were accepted. These featured indicator and preferential species that seem to indicate difference in moisture and shade. No habitat type was restricted to a single TWINSPAN community in the restricted sites dataset. TWINSPAN classification of forested sites (not shown) was deemed not to reflect community ecology more accurately than habitat types defined by overstory, and was therefore not pursued further.

TWINSPAN communities (full dataset) generally did not coincide with conservation hotspots to a greater degree than habitat types, with no fewer than three communities represented in the top richest sites for all conservation criteria, and many community types represented in the poorest sites (Figure 3.7). Every community type featured species that were not found in any other community type. Most of these species were found in *H. aeneum*, (e.g. *Campylium halleri*, *Metaneckera menziesii*, *Pohlia filiformis*, *Plagiopus oederiana*), *B. erythrorrhizon* (e.g. *Polytrichum commune*, *Rhytidiadelphus squarrosus*, *Sphagnum teres*, *Pohlia sphagnicola*) and *D. aduncus* (e.g. *Climacium dendroides*, *Leptodictyum humile*, *Plagiomnium*

cuspidatum) communities (Table 3.6). The fewest species were exclusive to *W. controversa*, *B. velutinum*, and *P. piliferum* communities, and these were all found in just one site each.

Significant differences in conservation value were fewer among community types than for habitat types (Table 3.7), but high and low values for each criterion were significantly different. High mean richness was observed in *Homalothecium aeneum*, *Tortula norvegica* (rocky) and *Brachythecium erythrorrhizon* (flowing water) communities (Table 3.7). In unrestricted habitats, *Brachythecium hylotapetum*, *Amblystegium serpens* (forested) and *Drepanocladus aduncus* (wetland) communities featured the greatest mean richness. These conservation values were also high in the *Amphidium lapponicum* community, which was characterized by species preferring wet, sheltered rock. Western North American endemic species were most numerous in mesic coniferous forest communities (*Mnium spinulosum* and *Brachythecium hylotapetum*) and in permanent streams (*Bryum weigelii* community). *Brachythecium hylotapetum* and *Brachythecium erythrorrhizon* communities were among the three sites with the greatest conservation value for all criteria. *Drepanocladus aduncus* communities featured high mean numbers of locally rare species. No significant difference in mean conservation value was detected among the three restricted site communities.

The greatest gamma diversity for all TWINSPAN communities defined for all datasets is projected for sites supporting *Amphidium lapponicum* communities (Figure 3.8). Gamma diversities of the other two restricted habitat communities were similar to each other and to the communities derived from all sites that displayed high gamma diversity – *Homalothecium aeneum*, *Brachythecium erythrorrhizon*, and *Tortula norvegica*. *Brachythecium hylotapetum* and *Amblystegium serpens* communities achieved the greatest gamma diversity among the unrestricted habitats, but the species / sampling effort curve for *Amblystegium serpens* would be soon overtaken by *Mnium spinulosum* if the lines were extrapolated (Figure 3.8).

Beta diversities are difficult to project for TWINSPAN communities as the rank of each community with respect to gamma diversity is likely to have changed with increased sampling effort (Figure 3.8). *Drepanocladus aduncus* and *Brachythecium erythrorrhizon* feature the highest species turnover of communities derived from the full dataset (Figure 3.9.A). These coincided largely with peatland and stream habitats which showed high species turnover in the analysis of habitat types. The greatest species turnover was similar (Figures 3.9.A,B, n=15) for communities derived from all sites and from unrestricted habitats.

Among unrestricted habitats, *Lescuraea radicosa* and *Drepanocladus aduncus* communities showed the highest beta diversities. These values exceeded that of the *Bryum weigelii* community, which featured the highest species turnover among communities derived from restricted habitats, at a lower sampling effort (Figures 3.9.B,C).

3.4.4 Patterns of conservation value with respect to compositional and environmental gradients

The first three ordination axes were important in explaining variation in the full dataset, whereas the first two axes accounted for most of the variation explained in unrestricted, restricted, and forested habitats (Table 3.8). Up to 76% of the variation in the species data was explained in the ordinations (Table 3.8). Species-environment correlations were high (minimum 0.76) for all axes that explained more than 5% variance. Low eigenvalues (Table 3.8) were an artifact of the Beals smoothing process, and do not affect the amount of variation explained in this analysis.

When all sites were ordinated, wet communities generally separated from dry communities along axis 1 (Figure 3.10.A., B.), which was positively correlated with moisture, bryophyte cover, and stability, and negatively correlated with percent cover of rock (Table 3.9). *D. aduncus* and *B. erythrorrhizon* communities were concentrated at opposite ends of axis 2, which was negatively correlated with coniferous tree cover, elevation, and proximity to the continental divide (Figure 3.10.A.,B., Table 3.9). The forested communities (*M. spinulosum* and *B. velutinum*) were largely restricted to the low end of axis 3, which corresponded to high litter depth and high percent cover of herbaceous plants and soil substrate, and low habitat complexity (Figure 3.10.B.,C., Table 3.9). An especially large degree of overlap between dry communities was observed on the ordination diagram. The *M. spinulosum* community displayed the greatest spatial definition of all the dry communities, favouring conditions negatively correlated with axes 2 and 3 (Figure 3.10.C).

Quantitative overlays of conservation value on ordinations of the full dataset were characterized by poorly-defined trends (Figures 3.10.D.-G.) substantiated by generally low correlations of conservation value with ordination axes (Table 3.9). Ordinations of all sites overlaid with site richness (Figures 3.10.D.-E.) showed no obvious patterns, although there was a significant, negative correlation with axis 2 (Table 3.10). A concentration of sites with high numbers of locally rare species corresponded to very wet communities

(Figure 3.10.F, Table 3.10), but there were several dry community exceptions. Numbers of provincially tracked and S1 species were both negatively correlated with axis 2, but differed in the strength of their association with axes 1 and 3 (Table 3.10). Sites poor in locally rare species, provincially tracked and S1 species were evenly distributed throughout the ordination diagrams (Figures 3.10.F.-H.). Richness of western North American endemic species showed the most spatial resolution on the ordination of all sites (Figure 3.11.I), with a concentration of endemic species richness at high values of axes 1 and low values of axis 2 (Table 3.10).

The ordination of unrestricted habitat types was similar to that of all sites. The wet *D. aduncus* community segregated from dry communities along axis 1 (Figure 3.11.A), which was positively correlated with moisture and percent cover of water, and negatively correlated with slope and degrees longitude (Table 3.9.B). Among the dry communities, largely forested (*B. hylotapetum, P. lyallii, A. serpens*) and largely unforested (*L. radicosa, P. bolanderi, P. incurvata)* communities were centred at low and high values of axis 2 (Figure 3.11.A) respectively. Axis 2 was negatively correlated with stability and percent cover of organic soil and bryophytes (Table 3.9.B). Site richness was slightly negatively correlated with axis 2 and slightly positively correlated with axis 3 (Figures 3.11.B.,C., Tables 3.9.B, 3.10). Numbers of locally rare species (Figure 3.11.D) showed higher correlations with ordination axes than on ordinations of all sites (Table 3.10) and greater spatial resolution on ordination diagrams (Figures 3.11.D). Number of provincially tracked species (Figure 3.11.E) was negatively correlated with axis 2 (Table 3.10). Richness of locally rare and S1 species (Figure 3.11.F) were concentrated at opposite ends of axis 1 (Table 3.10), and generally showed stronger correlation with ordination axes than in the ordinations of all sites. Number of western North American endemics was also more strongly correlated with ordination axes, and was highest in sites at the high-stability end (Table 3.10) of axis 2, and the high elevation end of axis 3 (Table 3.10, Figure 3.11.G).

B. weigelii and *H. aeneum* communities occupied distinct zones of the ordination of restricted sites, with sites of *A. lapponicum* community type fell between these zones and overlapped them both (Figure 3.12.A). Axis 1 was correlated to most of the significant environmental variables (Figure 3.12.A, Table 3.9.C), with high values corresponding to high percent cover of bryophytes, high moisture, high elevation, low percent cover of rock, low elevation, and shallow rock microtopography. Moss species

richness (Figure 3.12.B), richness of locally rare species (Figure 3.12.C), and richness of western North American endemics (Figure 3.12.B) were positively correlated with axis 2 (Table 3.10). Provincially rare (Figure 3.12.D) and S1 (Figure 3.12.E) species showed opposite signs of correlation with axis 1 (Table 3.10), although the correlation of axis 1 with number of S1 species was not significant (Table 3.10). Number of provincially tracked species did not reflect the correlation of richness with axis 2. High numbers of western North American endemic species are positively associated with axis 1 (Table 3.10, Figure 3.12.F). No conservation values were correlated with axis 3 (Table 3.10).

Deciduous and coniferous sites separated according to their respective canopy type along axis 1 of the ordination of forested sites, with mixedwood sites occurring in between (Figure 3.13.A). Elevation and longitude were also positively correlated with axis 1 of the ordination (Table 3.9.D). Most quantitative overlays of conservation value demonstrate the paucity of species and rare species in most deciduous forest sites (Figures 3.13.B.-F.). Number of locally rare species showed no pattern with respect to ordination axes (Figure 3.13.C). The number of provincially tracked, S1, and western North American endemic species were positively correlated with axis 1. Species richness (Figure 3.13.B), number of tracked species (Figure 3.13.C) number of S1 species (Figure 3.13.E) and number of western North American endemics (Figure 3.13.F) were highly positively correlated with axis 2.

3.5 Discussion

3.5.1 Conservation hotspots

Inventoried sites known to possess high moss conservation value in Waterton should be preserved. Sites of high moss conservation value doubtlessly occur in the unsampled majority of the park, and decisions for uninventoried land should be made with reference to correlation of conservation value with habitat, community, and environmental cues gleaned from patterns existing among inventoried sites.

The clumped distribution of conservation hotspots contrasts with the even spread of coldspots (Figure 3.2), suggesting that greater predictability exists for high conservation value. This trend is mirrored in quantitative overlays of CCA ordinations, in which sites of high conservation value occupy distinct regions of an ordination diagram, but are interspersed with sites of low conservation value which occur in all regions of the diagram (e.g Figures 3.10.H, 3.11.D). Conservation based on patterns of rarity/richness

distribution will therefore be somewhat inefficient: if all sites displaying the biotic or abiotic characters of sites with high conservation value are preserved, a certain number of sites of low conservation value will also be preserved.

The majority of sites supporting moss richness and high numbers of rare moss species in Waterton were detected in the southwest corner of the park. This part of the park was very heavily sampled (Figure 3.2), and although this probably reflects, in part, a high trail concentration, it probably also relates to the high concentration of available habitat types. Unrestricted habitat types occur throughout the park, but restricted sites largely occur in the southwest (Figure 3.2), leading to greater mesohabitat and microhabitat diversity there. This finding supports the assertion by Vitt and Belland (1997) that (provincially) rare species occurrence is a function of the occurrence and diversity of mesohabitats and the number of particular mesohabitats. Waterton regions characterized by a high variety of habitat types should be conserved to maximize the preservation of different conservation values within the park.

Although several sites have high conservation value according to several criteria (Figure 3.1), at least three of the top 9-12 sites were important according to only one criterion. The fact that sites remarkable for different conservation criteria cluster together on the Waterton map suggests that, at least to some extent, richness and different kinds of rarity are spatially related beyond the statistical probability that sites with high numbers of species will house more rare species. Broad-scale regional factors are likely at play – for example, the majority of moss conservation hotspots in Waterton coincide with the zones of greatest precipitation (Poliquin 1973), with regions dominated by coniferous forest, with areas underlain with (often exposed) bedrock, and, as noted above, with high numbers of habitat types. Conversely, regions with the least moss conservation value occurred in the north east, where these factors are absent.

The fact that many closely-occurring Waterton moss conservation hotspots were remarkable for just one conservation criterion also indicates that different conservation values are not strictly distributed in tandem, and that fine scale features, perhaps partly of substrate and environment, must determine their occurrence. Prendergast et al. (1993) showed that conservation 'hotspots' for liverwort richness and rare species in Britain often did not coincide. Similarly, hotspots for moss richness often do not co-occur with high numbers of rare species in this study, despite their broad spatial correlation on a larger scale (Figure 3.2.A), and their statistical correlation from site to site (Table 3.5). Conservation of all hotspots of moss

species richness would ensure the preservation of no more than half the hotspots for any type of rare species (Figure 3.2.A). Preservation of all hotspots for one type of rare species would result in the preservation of an even lower proportion of hotspots for other conservation criteria (Figure 3.2.A). In many cases, sites of exceptional conservation value occur adjacent to those exceptionally low in conservation value, further suggesting that strong local habitat and environmental correlations determine favourability for overall species richness and/or richness of rare species.

Lack of a strong coincidence of the three rarity criteria in this study is expected because determinants of rarity vary among spatial scales. For example, wetland species (e.g. *Calliergon giganteum, Catascopium nigritum, Climacium dendroides, Dicranum undulatum, Drepanocladus exannulatus, Hypnum pratense, Sphagnum riparium, Sphagnum squarrosum*) were locally rare in Waterton due to the low number of peatland habitats in the park in conjunction with high peatland species turnover (Figure 3.5). Peatlands are common in Alberta, so peatland species are provincially common. Alternately, some species may be rare in Alberta because the continental divide and the eastern edge of the Rockies present a climatic and physical barrier to eastern range extension (e.g. *Brachythecium hylotapetum, Claopodium bolanderi, Heterocladium procurrens, Polytrichum lyallii, Roellia Roellii, Rhytidiopsis robusta*)(Vitt unpublished). The maritime climate of some Waterton sites supports some of these species in localized abundance. As a result, lists of locally and provincially rare species in Waterton are quite different, reflecting different ecological affinities. In the absence of a convenient interdependence of different kinds of moss conservation value (within Waterton regions housing high richness and rarity), the degree to which different conservation priorities are met by the application of different site-specific management decisions requires careful attention.

Hotspots for western North American endemic species occurred near the continental divide at relatively sheltered, low elevation sites. The endemic species found in this study are largely of temperate (e.g. *Coscinodon calyptratus, Atrichum selwynii, Pseudoleskea atricha, Brachythecium frigidum*) and montane (e.g. *Dicranum pallidisetum, Brachythecium hylotapetum, Rhytidiopsis robusta, Roellia roellii*) affinity, making these kinds of habitats best suited to endemic species growth. Many Canadian western North American endemics are most common in British Columbia and do not extend east of the Rockies (Schofield 1969), a factor which may also contribute to the proximity of these sites to the Continental

divide. Hotspots for western North American endemics showed no affinity for west-facing slopes, where the Waterton climate is reported to have the greatest maritime influence (Ogilvie 1962; Lopoukhine 1970).

Five of ten hotspots for locally rare species were wetlands, accounting for their occurrence in the east part of the park, away from the main concentrations of high conservation value (Figure 3.2). Wetland habitats themselves were not locally rare in this study (14 examples sampled), making the affinity of locally rare species for these habitats initially confusing. High variability among wetland habitats, even geographically close ones, however, helps to explain the trend (discussed later),

Vitt and Belland (1997) report that species designated 'S1' by ANHIC were more likely to be acrocarpous, stress tolerant, and of montane and temperate affinity than Alberta's more common species. Substrates of S1 species were almost exclusively rock and soil. Hotspots within Waterton for provincially rare species (S1 and S2 species, for a more recent tracking list) are not of particularly high elevation or extreme environment, but are all streams and cliff habitats, which would be relatively harsh compared to the forested matrix of the west part of the park. They are dominated by rock and soil substrates, while wood, living and dead, is conspicuously sparse. Although Vitt and Belland (1997) note the high contribution of alpine habitats to rare species occurrence, Waterton is home to much fewer arctic/alpine species than mountain parks to the north (chapter 2), so habitats important to rare temperate and montane species are more likely to be important in Waterton in particular – habitats that are more sheltered and mesic. Twenty-eight percent of Waterton's provincially rare species are endemic to western North America and another 24% are of boreal affinity (Chapter 2), accounting, in part, for their congregation in forested regions of the park.

3.5.2 Conservation value of habitat types

Some useful indicators of conservation value can be gained by comparing habitat types. Vitt and Belland (1997) base their model for the occurrence of provincially rare Alberta moss species on habitat types. They describe restricted habitats as the most important landscape component maintaining rare bryophyte species diversity, citing the abundance of microhabitats as a key determinant of rare species richness. Restricted habitats in Waterton also appear to be of paramount importance for the maintenance of (rare) species diversity. Restricted habitats in Waterton were home to significantly greater conservation

value than were unrestricted habitats, according to every conservation criterion (Table 3.3), and featured significantly greater habitat complexity. Bryophytes occur in close association with microhabitat conditions, so the comparatively wide variety of micro-environmental and edaphic conditions supplied by cliffs and streams is likely to support a wide variety of moss species. It is also likely to provide at least several places where mosses can 'escape' the environment of the site or of the park as a whole – places which support rare moss species. Interestingly, Heikkinen (1996) found that cliffs and streams were important reservoirs of vascular plant species richness in a Finnish park.

In considering restricted and unrestricted habitats separately, patterns of conservation value that were masked in examinations of the entire dataset were detected and/or enhanced. Correlations of conservation value with ordination axes ameliorated in several cases (Table 3.10). Correlation of conservation value with axis 1 (moisture) varies in strength, and in some cases in sign, between restricted and unrestricted datasets (Table 3.10). Designation of a site under consideration as representing a restricted or unrestricted habitat type could be used as a 'first cut' determining what patterns of conservation value should subsequently be applied.

Patterns of conservation value seem to be more clear for unrestricted habitats than for restricted habitats. Fewer significant correlations are observed between conservation value and axes of the restricted habitat ordination. Visually, one can see greater spatial fidelity of high conservation value on ordinations of unrestricted habitat types than on ordinations of all sites (e.g. Figures 3.10.G & 3.11.C, 3.10.I & 3.11.E). Several factors may be responsible for this trend: 1) Habitat heterogeneity is a primary correlate of richness in many systems (e.g. Crites & Dale 1997; Gould & Walker 1999; Huston 1994; Jonsson & Esseen 1990; La Roi & Stringer 1975; Lee & La Roi 1979; Newmaster 2000; Vitt et al. 1995). Perhaps other site factors such as environment become important only in the less complex sites. In particularly complex sites, more microhabitats may exist that do not reflect environmental variables measured at the site scale, whereas habitat and general site environment may be much better correlated in unrestricted habitats. 2) Perhaps the environments and communities of restricted mesohabitats are complicated by the environment of the broader unrestricted habitat matrix in which they are embedded, giving them less spatial integrity in ordinations and weakening correlations that exist in unrestricted mesohabitats. 3) Gradients of conservation value are more difficult to isolate when conservation value is consistently high. 4) More

unrestricted habitats were sampled, leading to the detection of stronger patterns. Regardless of the mechanisms at play, restricted habitats should be conserved due to their high conservation value, while unrestricted habitats should be examined with respect to additional factors.

In the current study, six habitat types – streams, mixedwood, coniferous forest, forested cliff, unforested cliffs, and wetlands – consistently recurred among moss conservation hotspots and habitat types (Figure 3.3) of high mean conservation value (Table 3.3). These habitat types generally supply a wide variety of substrates and microhabitat conditions for moss growth. However, examples of these habitat types (excluding forested cliffs) also exist among conservation cold spots, and statistical differences in mean conservation value between habitat types are few. In other words, it appears that sites of high conservation value are predictably of certain types, but that habitat types are not themselves predictably rich. This trend mirrors the contrasting spatial fidelity of sites with low and high conservation value on the Waterton map and on CCA ordinations, noted above. Conditions under which high conservation value is unlikely to occur are thus easier to define than conditions under which high conservation value *will* occur. Park managers should be aware of the potential site conservation value of the recurring six habitat types defined in this study, but additional predictors of conservation value may also be developed to refine predictive accuracy.

In most cases, site types designed to achieve thorough sampling of representative Waterton moss communities did not accurately reflect resident moss communities. Neither moss species composition nor environmental character was well correlated with most moss habitat types in TWINSPAN classifications (Figures 3.6.A-C) and on ordination diagrams (not shown). The majority of significant correlations of conservation value with ordination axes did not reflect discrete habitat types, and reflected instead environment and species composition factors transcending habitat type divisions. Furthermore, habitat types were defined in large part by dominant vascular vegetation, which is not necessarily related to bryophyte species richness, rarity, or composition (eg. Bradfield & Scagel 1984; Dirkse & Martakis 1998; McCune & Antos 1981; Pharo et al. 1999; Ryan et al. 1998; Zamfir et al. 1999). Simply conserving examples of each habitat type may not maximize moss species protection in Waterton Lakes National Park. More reliable correlates of moss species composition are required, both for inventory sampling and for management applications.

In a few cases in this study, however, habitat types were particularly important in determining conservation value. The segregation of locally rare species at the high end of moisture axes (Figures 3.10.G, 3.11.C) on ordinations of all sites and unrestricted sites results largely from the occurrence of peatland sites in this region of the diagrams. Similarly, on ordinations of forested sites, the low conservation value of deciduous forest contributes greatly to significant correlations with axes 1 and 2 (e.g. Figures 3.13.B,D). These habitat types were among those that segregated well from other habitat types on ordinations (Figures 3.11.A (*D. aduncus* community is made up largely of peatland sites), 3.13.A). Moss community composition, environment, and conservation value are presumably strongly linked for these habitats.

These qualities are linked in wetland and stream habitats in another way as well – they featured many species that were exclusive to the habitat type *and characteristic of it*. By conserving examples of wetland and stream habitat, park managers will conserve species that would be placed at risk if the habitat type as a whole were excluded from the park.

Wetlands and streams displayed high alpha and beta diversity. Streams may represent a particularly broad suite of site moisture and substrate conditions: water may flow throughout the year, or only during spring runoff, and it may flow slowly through a stable, organic forest floor or rush quickly down a steep slope, removing all but the coarsest mineral substrate. High turnover in wet habitats is corroborated in CCA ordinations in the form of the high spatial variation among moist sites compared with dry sites (e.g. Figure 3.10.A). Species turnover was otherwise greatest in habitat types that were generally low in alpha diversity (e.g. coniferous scrub and deciduous forest) . To preserve the floristic character of a park, it is important to conserve a larger number of habitats representing types with high turnover than habitats with low turnover if the gamma diversity for a given habitat type is to be conserved.

3.5.3 Conservation value of moss communities

The general failure of habitat types to accurately differentiate Waterton moss species composition or conservation values inspired the attempt to create and compare community groupings based on species composition rather than habitat features, in the hopes that, were conservation value associated with community type, these differences would be more clearly exposed. TWINSPAN communities derived from

all datasets could be readily interpreted in terms of the ecological preferences of indicator and preferential species. The close association of mosses with their environments should ensure that site ecology is accurately reflected by the species present. The single site visit characteristic of inventory work can introduce considerable subjectivity to estimates of explanatory variables. Associations between conservation value and environment should be more clearly revealed in correlations of community with conservation value. Low agreement between TWINSPAN communities and habitat types (Figures 3.6.A-C) confirmed that factors important to species composition are not immediately obvious in the field. If moss communities reliably predict conservation value, however, then a site may be assessed based on the presence of indicator or preferential species. This is more time-consuming and requires more technical expertise than identifying habitat types, but is still much easier than completing a full inventory.

However, the results of this study suggest that moss communities as defined by TWINSPAN are less reliable than habitat types for predicting moss conservation value in Waterton Lakes National Park. Conservation value is more variable (standard deviation, Tables 3.3, 3.7), and there are fewer significant differences in mean conservation value (Tables 3.3, 3.7), fewer large differences in beta diversity (Figures 3.5, 3.9), a lower range of gamma diversity (Figures 3.4, 3.8) among communities than among habitat types. Differences in beta and gamma diversity also reflect continua rather than sharp contrasts. This may indicate that conservation value and species composition are in most cases not closely related. This, in turn, may help to explain the low correlation of most conservation values with most ordination axes.

Newmaster (2000) reported moss conservation value with respect to moss communities. Species composition differed significantly between ages and types of British Columbia rain forest, and communities defined by cluster analysis from the same data also displayed significant differences in richness and numbers of rare species. Similarly, Vitt et al. (1995) found that different peatland bryophyte communities displayed important differences in species turnover and predictability, and that site diversity was related to environmental factors in different ways for different community types.

3.5.4 Gradients of species composition, environment, and conservation value

That different patterns of significant correlation with ordination axes are displayed for different conservation values in this study verifies the existence of gradients of conservation value related to species

composition and explanatory variables. An ordination not showing a pattern in site richness may show a lack of correlation of high species richness with ordination axes, and may often display a cluster of high values near the centre of the ordination diagram. Sites with lower richness generally occupy the periphery, since they will statistically share fewer species. Sites with high numbers of species of high conservation interest may be expected to show the same pattern of distribution as high site richness on ordination diagrams, as sites with more species are more likely to have more of any given species type.

A high percent of variance in the species data was explained in CCA ordinations (Tables 3.8A-D), suggesting that patterns of conservation value with respect to species composition, if present, would be detected. High species/environment correlations (Tables 3.8A-D) indicate that the environmental variables selected are appropriate for explaining variation in species composition. Patterns of site distribution on CCA ordinations result from species and environmental site characters. Thus, the quantitative overlays produced in this study reveal gradients of conservation value with respect to species composition and environment. Where strong correlations between gradients exist, park managers may be able to use environmental cues to rank sites for conservation. Clear patterns of conservation value transcending habitat and community boundaries were visible on ordinations in several cases.

High frequency of correlation of conservation value with axis 2 of all ordinations – an axis generally not accounting for a lot of variation in species composition (favourability) data – gives further evidence that conservation value relies most on factors of secondary importance to patterns of species occurrence and association. Those conservation values displaying high correlations with axis 1 are more likely to be patterned through strictly ecological mechanisms. Significant correlations of conservation value with axis 3 were observed only in ordinations in which axis 3 contributed significantly to explaining variation in species composition, suggesting that some ecological context for conservation value must exist.

That species richness is only significantly correlated with axis 2 for all ordinations is in keeping with the patterns of conservation hotspots on the Waterton map (Figure 3.2.A). Proximity to the continental divide (longitude) is highly negatively correlated with axis 2 in ordinations of all sites and of unrestricted habitats. Regions close to the divide are on average higher in elevation, and feature a greater variety of habitat types than areas in the east part of the park. Elevation is also highly negatively correlated with axis 2 of the ordinations of the full dataset. Areas near the divide also receive higher average precipitation, but

moisture was primarily associated with axis 1. Elevation and moisture have been related to conservation value by previous researchers. White and Miller (1988), for example, related vascular plant richness to elevation in the Appalachians, and Heikkinen (1998) found that altitudinally-related variables helped to explain the occurrence of rare vascular plant species in a Finnish Lapland. Frisvoll and Prestø (1997) report the preference of rare species in Norway for humid forests, and Gould and Walker (1999) found that bryophyte richness was positively correlated with moisture along an arctic river. Other important environmental correlates of axis 2 included coniferous tree cover (full dataset, restricted habitats, and forested habitats), cover of organic substrate (unrestricted and restricted habitats), shrub cover (full dataset, unrestricted habitats, restricted habitats), and bryophyte cover (unrestricted and restricted habitats). These variables appear infrequently in the literature.

Number of western North American endemic species was significantly, positively correlated with axis 1 of ordinations of all but the unrestricted habitat dataset, and locally rare species were positively correlated with axis 1 of ordinations of all sites and unrestricted habitats. As noted above, western North American endemics and locally rare species in Waterton each are united by certain ecological preferences. Locally rare species were well-represented in peatlands, which are only included in the two datasets for which correlations with axis 1 were observed. Western North American endemics were consistently correlated with two ordination axes, and generally displayed the highest correlations with ordination axes. Similarly, particularly low correlations observed for richness likely reflect the wide ecological variety represented by the species in this study. Axis 1 consistently represents moisture and slope in full, restricted, and unrestricted datsets. Percent cover of organic soil is greater in axis 2 of the ordination of unrestricted habitats, but is greatest in axis 1 ordinations of full and restricted datasets. The preferred substrate of many endemic species in this study is soil or debris, contributing, perhaps, to the absence of a significant correlation of endemic species richness with axis 1 of the unrestricted habitat ordination.

3.5.5 Remarks on approach to inventory and exploration

All site and species data subsets explored in this study revealed hidden patterns in conservation value, suggesting that a tiered approach to predicting site conservation value may be appropriate. The selection of data subsets has the effect of controlling for certain factors, because these subsets are defined

based on key physical or biotic features. For example, longitude probably becomes unimportant in the ordination of restricted sites because most restricted habitats occur in a relatively narrow, western band. Complexity, similarly, became individually insignificant (and was thus excluded before ordination) for explaining differences in species composition among restricted habitats. In short, certain factors may be important for determining the conservation value of the dataset as a whole and may be used as a 'first cut', while others differentiate between conservation values within the dataset. These patterns more accurately reflect the true distribution of species composition and conservation value on the Waterton landscape than patterns in the whole dataset, but the treatment subdivisions reduces sample size and thus the strength of any implied patterns, and introduces considerable complexity to their application by park managers. A compromise between complexity and predictability must be struck through the judicious selection of subdivisions.

It was intended that habitat types, which formed the basis of comprehensive sampling in this study, would approximate moss communities, but they did not. Species-sampling effort curves corroborate the failure of site types to properly direct sampling. Species detection did not level off within the sampling effort devoted to any subset of the sites sampled (Figures 3.3A-C). The curve for all sites is the closest to becoming horizontal, suggesting that park moss diversity is closest to being adequately assessed in this study. The diversity of individual habitat types and communities in Waterton has not been captured, and future work may benefit from the identification of more effective, efficient sampling units.

Standardizing site size in this study, or within different habitat types may also lend reliability to the interpretation of results. Many researchers standardize sampling and simplify interpretation by focusing on a single community type. This approach is far less useful in a park management context than investigations encompassing the range of variability within a park, but it would allow for a more detailed and thorough understanding of diversity and rarity relationships in the ecological setting selected. In the current study, separate consideration of forests did show different general patterns compared with the full dataset. Some researchers (eg. Heikkinen 1998; Miller 1986; Richerson & Lum 1980) who employ a comprehensive approach apply a grid system to their study area, thereby considering environmental and species data from the entire jurisdiction. This is only possible with large sampling effort and/or data that can be interpreted from maps or air photos rather than by field reconnaissance.

In this study, environmental variables unimportant to species composition were generally ignored when looking for variables important for conservation value. Habitat complexity, for example, which is a well-documented correlate of species richness, operates by providing a variety of habitats rather than conditions favourable to specific ecological preferences. Furthermore, when species composition and conservation value were unrelated, no correlation between environment and conservation value could be pursued. Predictive modelling of richness and numbers of rare species has been undertaken by several authors, and may further elucidate and more accurately quantify patterns of moss conservation value with respect, exclusively, to environmental cues in Waterton Lakes National Park.

3.6 Management recommendations

Management recommendations are made with two scenarios in mind: decisions for land use encompassing or traversing regions (groups of sites) of the park, and decisions for land use where several individual sites are under consideration. It is assumed that park managers are concerned with preserving a high number of species and rare species and with maintaining the floristic character of the park. Supposing that a number of potential sites are under consideration for development, then, a manager must not only compare the numbers of species supported in each site, but also the degree to which each site contributes to Waterton's conservation value. If, for example, one site represents a habitat type characterized high site diversity but low turnover, it may be less important for Park diversity than a site representing a habitat type characterized by high species turnover or high numbers of species exclusive to the habitat type.

3.6.1 Inventoried sites

1. Sites shown in this study to support high moss conservation value should be preserved. Preserving these sites will contribute to maintaining the site and regional diversity and floristic character of the park.

3.6.2 Un-inventoried sites

2. The conservation value of each site with respect to site richness and richness of locally rare, provincially rare, and western North American endemic species should be considered

separately because they do not reliably co-incide. Site-specific management decisions should reflect the prioritization of conservation values by park managers. If only one of these conservation values can be considered, site richness is most consistently correlated with other conservation values. Locally rare species are most likely to be under-protected by conserving only species-rich sites

3.6.2.1 On a park scale

3. Considerably more moss conservation value in Waterton occurs in regions characterized by a wide variety of habitat types – generally in the south and west areas of the park - which receive high annual precipitation and which are characterized by wide variation in dominant substrate, altitude, and forest cover.
4. To preserve western North American endemic species, preserve regions in the coniferous-forested western part of the park should be protected.
5. Provincially rare species share the fewest ecological traits, and therefore their richness is difficult to predict.
6. To preserve locally rare species preserve regions where peatlands are found, as in the south part of the park, should be protected.

3.6.2.2 On a site scale

7. Conservation value can be predicted based on habitat type. Restricted habitats should be conserved because they consistently support higher site conservation value according to all criteria, and because conservation value is more difficult to predict among restricted sites than among unrestricted habitats. Unrestricted habitat types require more detailed consideration with respect to management conservation priorities (scale, species of interest).
8. One simple (yet crude) way to determine what (kinds of) sites should be conserved and in what proportions is by considering differences in alpha, beta, and gamma diversity of inventoried sites. Sites with high alpha diversity and habitat and community types with high gamma diversity contribute many species to the overall diversity of the park. Habitat or community

types with high beta diversity require that more examples of these types be conserved in order to ensure the perpetuation of the species characteristic of these types.

9. Species composition is only closely related to conservation value and species composition in a few cases. Community types are more useful for characterizing species in a site, and less useful for determining conservation value than habitat types. If some species data is already available, community types may be useful for confirming predictions of conservation value.
10. Trends in conservation value transcending habitat and community types were observed in this study, and these trends were particularly strong in unrestricted habitat types. Habitat types may represent a useful 'first cut', but conservation priorities for unrestricted sites should ideally be considered with reference to their position on compositional or environmental gradients. These trends can be quantified and formalized in the form of predictive models.

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Table 3.1. Habitat types used to ensure diversity of moss sampling in Waterton Lakes National Park.

Habitat type	Definition
Coniferous forest	Overstory consists purely of coniferous trees
Deciduous forest	Overstory consists purely of deciduous trees
Mixedwood forest	Overstory consists deciduous and coniferous trees in a ratio of at least 25%:75% (or vice-versa)
Talus	Sloping rocky debris at the base of a cliff or exposed high elevations
Coniferous scrub	Overstory consists of patchy coniferous trees less than 3m high
Forested cliff	Cliff is shaded by forest overstory
Unforested cliff	Cliff is unshaded by forest vegetation
Alder	Overstory consists purely of Alnus spp.; steeply-sloping
Alluvial gravel	Flat mineral substrate (sand-coarse gravel) associated with rivers or streams; much substrate exposed. Overstory vegetation is sparse
Wetland	Flat or gently-sloping, peat- or organic-substrate, saturated at least in patches
Stream	Stream course and banks. May be intermittent or continuous within the summer season
Grassland	Dominated by graminoids, no more than 10% tree cover in any 10 x 10m area
Meadow	Treeless, high-elevation, non-rocky or minerally herbaceous community

Table 3.2. Environmental variables estimated at Waterton Lakes National Park moss sampling sites. Variables marked with an asterisk were not present at all sites, and thus were not used in all analyses. Codes are applied in CCA ordinations.

Estimated variable (units)	Code	Measurement methods
Position (degrees latitude & longitude)	LATITUDE LONGITUDE	Referred to Garmin GPS12 Global Positioning System unit
Aspect (degrees from northwest)*	ASPECT1 ASPECT2 ASPECT3	Took a compass bearing in the direction that the slope of the site faced. Aspect was transformed according to Beers et al. (1966) with respect to three 'favourable' aspects (1-3 respectively): south-west, north-west, and west.
Slope (degrees)	SLOPE	Sighted second researcher through a clinometer
Elevation (m above sea level)	ELEVATION	Referred to (details) digital altimeter
Site moisture (no units)	MOISTURE	Estimated on an arbitrary scale from 1 (dry) to 5 (wet)
Cover of water (% cover)	WATER	Estimated visually
Abundance of soil substrate (% cover)	SOIL	Estimated visually
Abundance of mineral soil (% cover)	MINERAL	Estimated visually, removing overlying litter where necessary
Abundance of organic soil substrate (% cover)	ORGANIC	Estimated visually, removing overlying litter where necessary
Abundance of exposed soil (% cover)	EXPSOIL	Estimated visually
Soil texture (no units)	SOILTEX	Estimated on an arbitrary scale from 1 (coarse) to 3 (fine)
Abundance of rock (% cover)	ROCK	Estimated visually
Abundance of exposed rock (% cover)	EXPROCK	Estimated visually
Rock roughness (no units)	ROUGH	Estimated on an arbitrary scale from 1 (fine) to 5 (coarse) with reference to sandpaper
Rock microtopography (no units)	MICROTOP	Estimated on an arbitrary scale from 1 (fine) to 5 (coarse) with reference to surface relief
Substrate stability (no units)	STABILITY	Estimated on an arbitrary scale from 1 (actively eroding) to 5 (stable)

Table 3.2 (cont'd)

Estimated variable (units)	Code	Measurement methods
Deciduous tree cover (% cover)	DECIDUOUS	Estimate visually
Coniferous tree cover (% cover)	CONIFER	Estimated visually
Tree height (m)	TREEHITE	Applied trignometry to angle (clinometer) and distance (measured paces) measurements (ref)
Abundance of dead wood (% cover)	WOOD	Estimated visually
Shrub cover (% cover)	SHRUBS	Estimated visually
Herbaceous plant cover (% cover)	HERBS	Estimated visually
Bryophyte cover (% cover)	BRYOS	Estimated visually
Litter thickness (cm)	LITTER	Averaged several ruler measurements
Habitat heterogeneity (no units)	COMPLEX	Counted the number of microhabitat features (list features) present

Table 3.3. Comparison of mean conservation value (± standard deviation) in different habitat types used to direct moss diversity sampling in Waterton Lakes National Park. Letters indicate homogeneous subsets according to Tukey post-hoc tests of ANOVA comparisons of means. Differences between restricted and unrestricted sites were significant for all criteria, using parametric tests (ANOVA) for richness, and number of provincially rare species and non-parametric tests (Mann-Whitney and Wilcoxon U) for the number of endemic species and locally rare species.

Habitat type	Mean site richness (α diversity)	Mean /Median Endemic	Mean Tracked	Mean /Median Locally Rare
Alder slope (4)	7.00 ± 2.12 a	0.50 ± 0.29 0.5	1.75 ± 0.48 a	Constant at 0
Meadow (4)	10.50 ± 3.97 ab	0.75 ± 0.25 1.00	2.50 ± 1.19 abc	0.25 ± 0.25 0.00
Grassland / Savannah (7)	11.57 ± 1.32 abc	0.29 ± 0.18 0.00	2.86 ± 0.55 abcd	0.43 ± 1.15 0.00
Coniferous Scrub (8)	13.50 ± 2.88 abc	1.13 ± 0.48 1.00	1.75 ± 0.65 ab	0.63 ± 0.26 0.50
Deciduous forest (7)	14.57 ± 4.55 abc	0.14 ± 0.14 0.00	1.00 ± 0.44 a	0.86 ± 0.70 0.00
Alluvial Gravel (5)	19.00 ± 3.92 abcd	0.40 ± 0.24 0.00	2.00 ± 0.84 ab	1.20 ± 0.37 1.00
Wetland (14)	19.57 ± 2.56 abcd	1.14 ± 0..39 1.00	2.36 ± 0.50 abc	5.43 ± 1.02 4.50
Talus slope (8)	20.25 ± 1.61 bcd	0.38 ± 0.18 0.00	3.13 ± 0.61 abcde	1.88 ± 0.48 1.50
Coniferous forest (17)	28.12 ± 2.51 cd	3.88 ± 0.33 4.00	5.00 ± 0.58 bcde	2.41 ± 0.49 2.00
Unforested Cliff (10)	32.70 ± 4.11 d	1.20 ± 0.25 1.00	7.00 ± 1.06 cde	4.43 ± 1.49 2.00
Stream (16)	35.25 ± 3.08 d	3.00 ± 0.42 3.00	8.19 ± 1.00 e	4.25 ± 0.68 4.00
Mixedwood (5)	35.60 ± 2.32 d	3.40 ± 0.24 3.00	4.80 ± 0.58 bcde	1.40 ± 0.51 1.00
Forested Cliff (7)	37.29 ± 5.06 d	3.00 ± 0.53 3.00	7.71 ± 1.44 de	2.90 ± 1.07 2.00
Restricted (33)	34.91 ± 12.45	2.45 ± 1.60 2.00	7.73 ± 3.70	3.88 ± 3.17 3.00
Unrestricted (79)	19.59 ± 11.05	1.53 ± 1.76 1.00	2.97 ± 2.22	2.03 ± 2.65 1.00

Table 3.4. Number of species in three conservation categories that were endemic to (occurred exclusively in) each of the habitat types sampled in Waterton Lakes National Park. Numbers in parentheses indicate the number of species that were found in just one site.

Habitat type	All Species	WNA endemic	Tracked	Locally Rare
Alder	0	0	0	0
Alluvial	3 (1)	0	2	3
Conifer	8 (1)	3	4	8
Coniferous Scrub	2	1	2	2
Deciduous	1	0	0	1
Forested Cliff	6 (1)	0	3	6
Grassland	2	1	2	2
Mix	0	0	0	0
Meadow	1	0	1	1
Stream	17 (10)	3	10	14
Talus	6	0	0	6
Unforested cliff	8	0	7	8
Wetland	24 (8)	0	6	24
Restricted	47	5	28	38
Unrestricted	55	7	19	46

Table 3.5. Correlation matrix (Kendall's tau-b) of moss conservation values measured in each of A. all 112 sites, B. 79 unrestricted habitats, C. 33 restricted habitats, D. 29 forested habitats in Waterton Lakes National Park. "Richness" refers to site alpha diversity, "Tracked" denotes the number of provincially tracked species, "Locally Rare" refers to the number of species occurring in five or fewer sites in Waterton, and "Western NA Endemic" refers to the number of species that are endemic to western North America. Asterisks show significance of correlation (*p<0.05, **p<0.001).

		Tracked	Locally Rare	Western NA Endemic
A	Richness	0.608**	0.480**	0.488**
	Tracked		0.473**	0.522**
	Locally Rare			0.327**
B	Richness	0.514**	0.415**	0.477**
	Tracked		0.367**	0.491**
	Locally Rare			0.267*
C	Richness	0.521**	0.505***	0.326*
	Tracked		0.533**	0.501**
	Locally Rare			0.345*
D	Richness	-0.73	0.356*	0.353*
	Tracked		-0.420	-0.230
	Locally Rare			0.412**

Table 3.6. Number of moss species that were found exclusively in each of eight moss community types in Waterton Lakes National Park. Numbers in parentheses indicate the number of species that were found in more than one site.

	All Species	WNA endemic	Tracked	Locally Rare
B. erythrorrhizon	19 (7)	1	4 (2)	19 (7)
B. velutinum	4	2	3	4
D. aduncus	11 (3)	0	5 (1)	11 (3)
H. aeneum	23 (8)	1 (1)	15 (4)	22 (7)
M. spinulosum	6 (1)	2 (1)	5 (1)	6 (1)
P. piliferum	4	0	1	4
T. norvegicum	9 (1)	0	5	9 (1)
W. controversa	1	1	1	1

Table 3.7. Comparison of mean conservation value (± standard deviation) in different TWINSPAN communities derived from A. All sites, B. Unrestricted habitats, and C. Restricted habitats in Waterton Lakes National Park. Community names match those on TWINSPAN dendrograms (Figures 3.6A.-C., respectively). Letters indicate homogeneous subsets according toTukey post-hoc tests of ANOVA comparisons of mean richness and number of tracked species. Other conservation criteria did not meet criteria required for parametric statistics. No significant differences in any mean/median conservation value were detected between communities derived from restricted habitats. Number of tracked species was log-transformed for comparing means between communities derived from the full dataset.

Twinspan Community	Mean α	Mean /Median Endemic	Mean Tracked	Mean/Median Locally Rare
A. All sites				
Brachythecium velutinum	10.88 ± 4.58 a	0.25 ± 0.46 0.00	2.63 ± 1.51 ab	0.50 ± 0.93 0.00
Drepanocladus aduncus	15.77 ± 10.24 ab	0.62 ± 0.96 0.00	1.69 ± 1.32 a	3.08 ± 2.63 2.00
Polytrichum piliferum	19.18 ± 10.19 ab	1.64 ± 1.36 1.00	4.45 ± 3.17 ab	2.09 ± 2.47 1.00
Mnium spinulosum	23.90 ± 13.94 abc	3.24 ± 1.95 4.00	4.38 ± 3.26 ab	1.71 ± 2.05 1.00
Weissia controversa	24.45 ± 13.40 abc	1.73 ± 1.42 1.00	2.91 ± 2.51 ab	1.09 ± 1.14 1.00
Brachythecium erythrorrhizon	25.73 ± 9.54 bc	2.53 ± 2.07 2.00	5.87 ± 4.45 b	4.73 ± 4.03 3.00
Homalothecium aeneum	29.30 ± 13.55 bc	1.60 ± 1.60 1.00	5.30 ± 3.57 ab	3.05 ± 3.15 2.00
Tortula norvegica	34.92 ± 14.12 c	1.31 ± 1.11 1.00	6.15 ± 3.89 b	3.15 ± 3.26 2.00
B. Unrestricted habitats				
Pseudoleskea incurvata	7.25 ± 4.65 a	0.5 ± 0.58 0.5	2.00 ± 0.82 a	Constant at 0
Pohlia bolanderi	11.14 ± 4.38 a	0.14 ± 0.38 0.00	2.86 ± 1.46 ab	0.43 ± 0.79 0.00
Lescuraea radicosa	15.47 ± 6.75 ab	0.47 ± 0.51 0.00	2.24 ± 1.64 ab	1.24 ± 1.20 1.00
Polytrichum lyallii	15.63 ± 8.7 ab	2.38 ± 1.30 2.50	3.63 ± 2.88 ab	1.50 ± 2.45 0.50
Drepanocladus aduncus	17.13 ± 9.87 abc	0.60 ± 0.91 0.00	1.80 ± 1.37 a	4.20 ± 3.57 3.00
Amblystegium serpens	27.15 ± 12.45 bc	1.46 ± 1.56 1.00	2.92 ± 2.60 ab	0.92 ± 1.12 1.00
Brachythecium hylotapetum	29.53 ± 8.47 c	4.20 ± 1.21 4.00	5.00 ± 2.10 b	3.27 ± 3.03 2.00
C. Restricted habitats				
Bryum weigelii	29.45 ± 11.64	3.18 ± 1.83 3	8.82 ± 4.29	3.64 ± 2.73 3
Encalypta procera	34.56 ± 11.25	2.56 ± 1.42 2	6.33 ± 2.96	3.33 ± 3.54 2
Amphidium lapponicum	39.77 ± 12.77	1.77 ± 1.30 2	7.77 ± 3.59	4.46 ± 3.41 4

Table 3.8. Summaries of canonical correspondence analyses of moss presence/absence data from four sets of sites in Waterton Lakes National Park: A. All 112 sites, B. 79 sites of unrestricted habitat types, C. 33 sites of restricted habitat types, D. 29 sites of forested habitat types. "Cumulative % variance" refers to percent variance explained in the species dataset. Species-environment correlations are Pearson correlations.

		Axis 1	Axis 2	Axis 3
A	Eigenvalue	0.084	0.048	0.034
	Cumulative % variance	24.8	38.8	48.8
	Species-Environment Correlation	0.891	0.804	0.887
B	Eigenvalue	0.093	0.039	0.007
	Cumulative % variance	41.6	59.2	62.4
	Species-Environment Correlation	0.870	0.878	0.771
C	Eigenvalue	0.063	0.006	0.003
	Cumulative % variance	66.2	72.4	75.6
	Species-Environment Correlation	0.953	0.926	0.700
D	Eigenvalue	0.019	0.003	0.001
	Cumulative % explained	49.1	56.5	58.3
	Species-Environment Correlation	0.865	0.759	0.568

Table 3.9. Intraset correlations between environmental variables and CCA LC scores for A. All sites, B. Unrestricted habitat types, C. Restricted habitat types, and D. Forested habitat types. Variable names are detailed in Table 3.2. Prefixes 'Arc', 'Log', and 'Sqrt' denote arcsin, log, and square root transformation, respectively.

Variable	Axis 1	Axis 2	Axis 3
A All sites			
LONGITUDE	0.008	-0.777	0.153
ArcSLOPE	-0.535	-0.251	0.199
LogELEVATION	0.029	-0.694	0.422
MOISTURE	0.811	0.184	0.271
SqrtLITTER	0.017	-0.126	-0.695
ArcWOOD	0.201	0.001	-0.521
ArcSOIL	0.300	-0.097	-0.641
ArcMINERAL	-0.312	-0.293	0.119
ArcORGANIC	0.566	0.068	-0.659
ArcROCK	-0.467	-0.097	0.661
STABLITY	0.520	0.009	-0.337
DECIDUOUS	0.066	0.339	-0.389
ArcCONIFER	0.070	-0.481	-0.420
ArcSHRUB	0.296	-0.157	-0.409
ArcHERBS	0.163	0.093	-0.502
ArcBRYOS	0.617	-0.181	0.121
WATER	0.506	0.302	0.314
COMPLEX	-0.220	-0.232	0.475
B Unrestricted habitats			
LONGITUDE	-0.492	-0.502	-0.260
SLOPE	-0.585	0.080	-0.153
ELEVATION	-0.471	-0.318	-0.535
MOISTURE	0.857	-0.398	0.034
SqrtLITTER	-0.147	-0.399	0.685
ArcSOIL	-0.017	-0.419	0.217
ArcMINERAL	-0.483	0.205	-0.291
ArcORGANIC	0.369	-0.550	0.433
LogROCK	-0.467	0.476	-0.138
STABLITY	0.383	-0.507	0.155
DECIDUOUS	0.164	0.055	0.614
CONIFER	-0.280	-0.423	0.243
ArcSHRUB	0.098	-0.447	0.362
ArcHERBS	0.099	-0.228	0.089
ArcBRYOS	0.413	-0.508	-0.072
WATER	0.750	0.018	-0.195
COMPLEX	-0.330	0.053	0.083

Table 3.9 (cont'd)

Variable	Axis 1	Axis 2	Axis 3
C Restricted habitats			
LONGITUDE	0.380	0.209	-0.333
ArcSLOPE	-0.646	-0.042	-0.456
ELEVATION	0.600	-0.219	-0.251
MOISTURE	0.729	-0.068	0.345
ArcSOIL	0.494	0.178	0.281
LogMINERAL	0.422	0.151	-0.018
LogORGANIC	0.537	0.387	0.181
ArcROCK	-0.505	-0.151	-0.346
MICROTOP	-0.567	0.035	-0.470
ArcCONIFER	0.140	0.757	0.219
ArcSHRUB	0.006	0.645	0.414
LogBRYO	0.564	0.403	-0.025
ArcWATER	0.526	0.067	0.479
D Forested sites			
LONGITUDE	0.869	-0.192	-0.317
ELEVATION	0.735	-0.528	0.425
DECIDUOUS	-0.801	-0.443	-0.192
CONIFER	0.567	0.759	0.267

Table 3.10. Pearson correlations between conservation value and CCA ordination axes in ordinations of four site datasets of moss species in Waterton Lakes National Park (*p<0.05, **p<0.001).

Dataset	Axis	Richness	WNAend	Prov. Rare	S1	Locally Rare
All sites	1	-0.012	0.208 *	0.022	-0.188 *	0.388 **
	2	-.258 **	-0.455 **	-0.353 **	-0.269 **	-0.054
	3	0.156	-0.137	0.360 **	0.126	0.173
Unrestricted habitats	1	-0.045	-0.183	-0.205	-0.292 **	0.453 **
	2	-0.247 *	-0.580 **	-0.288 *	-0.164	-0.287 *
	3	0.250 *	0.236 *	0.081	0.044	-0.152
Restricted habitats	1	-0.045	0.443 **	0.385 *	-0.183	0.124
	2	0.436 **	0.512 **	0.313	0.020	0.403 *
	3	0.122	-0.111	0.251	0.202	-0.004
Forested habitats	1	0.148	0.662 **	-0.323 *	0.427 *	0.278
	2	0.612 **	0.493 **	0.147	0.494 **	0.151
	3	-0.115	-0.088	-0.012	0.037	-0.112

Figure 3.1. Map of North America, with the star indicating the location of Waterton Lakes National Park, Alberta, Canada.

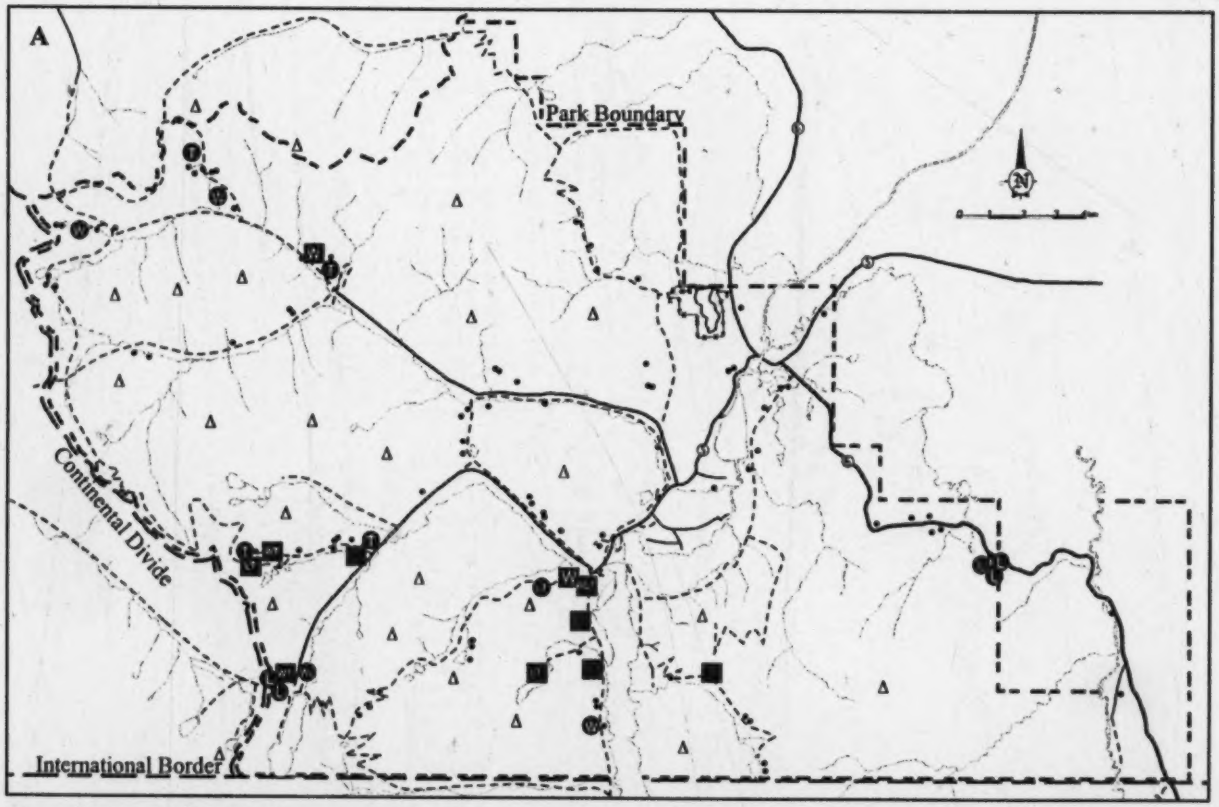


Figure 3.2.A. Distribution of moss conservation hotspots sampled in Waterton Lakes National Park. Squares indicate sites with the greatest richness, letters indicate sites with the greatest number of western North American endemic species (W), provincially-tracked species (T), and/or locally rare species (L). Small circles represent sites that were sampled but that were unremarkable with respect to high richness or number of rare species. Triangles indicate the locations of mountain peaks. Gray areas and lines represent lakes and rivers / streams respectively. Thin dotted lines depict trails and solid black lines represent roads.

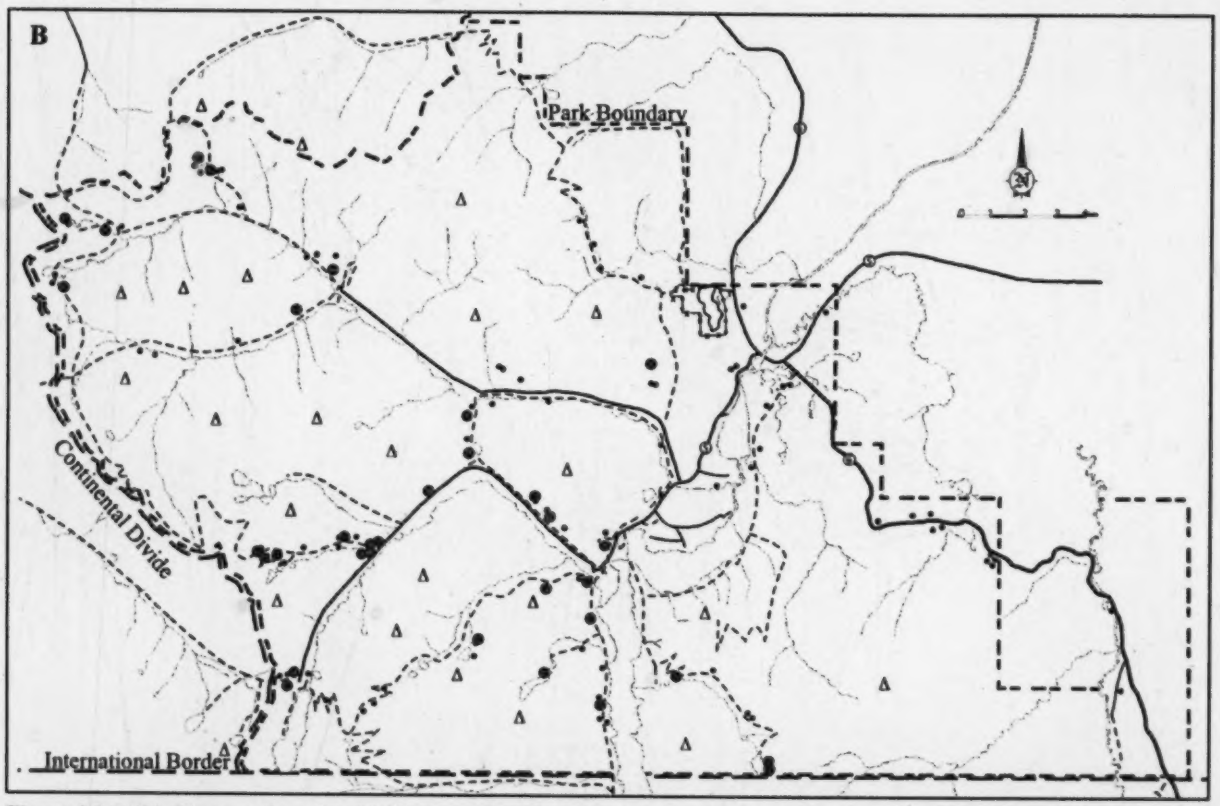


Figure 3.2.B. Distribution of restricted habitat types (cliffs and streams) sampled in Waterton Lakes National Park. Large circles indicate restricted habitats. Small circles represent unrestricted habitat types. Triangles indicate the locations of mountain peaks. Gray areas and lines represent lakes and rivers / streams respectively. Thin dotted lines depict trails and solid black lines represent roads.

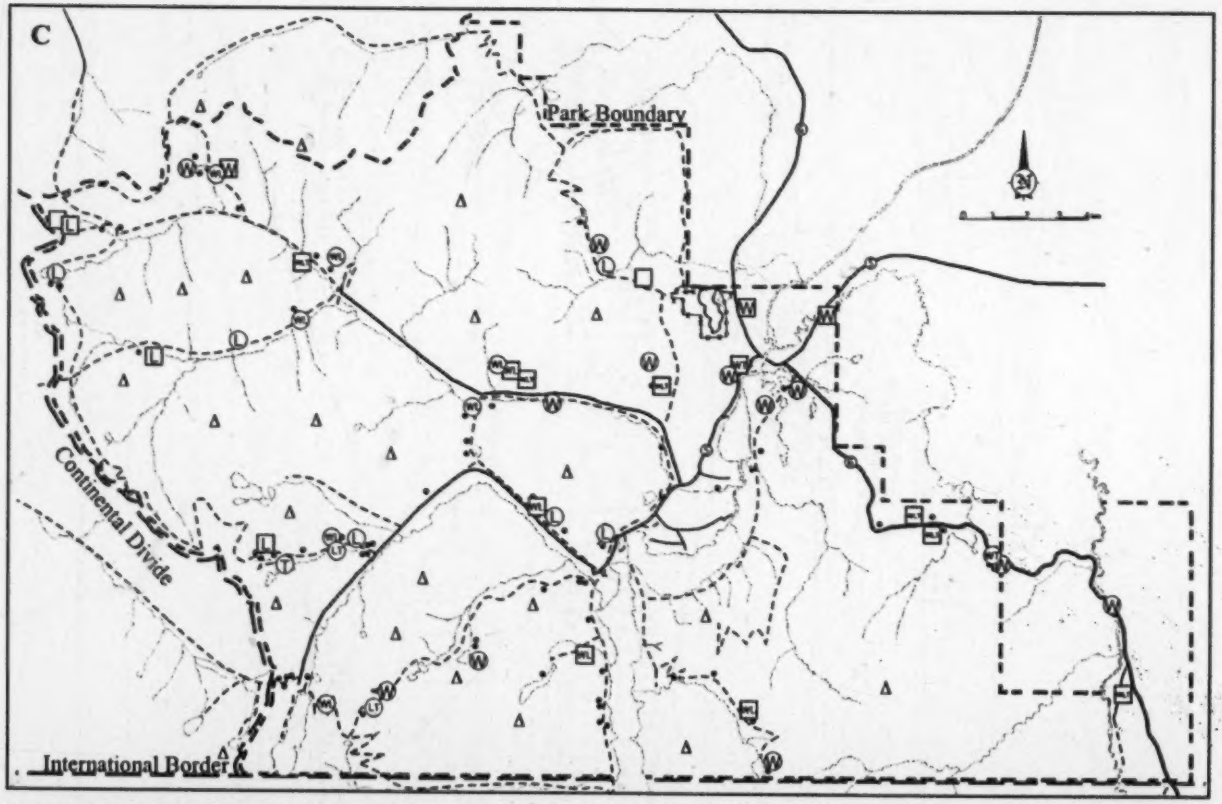


Figure 3.2.C. Distribution of moss conservation coldspots sampled in Waterton Lakes National Park. Squares indicate sites with thelowest richness, letters indicate sites with no western North American endemic species (W), no provincially-tracked species (T), and/or no locally rare species (L). Small circles represent sites that were sampled but that were unremarkable with respect to low richness or number of rare species. Triangles indicate the locations of mountain peaks. Gray lines represent rivers and streams. Thin dotted lines depict trails and solid black lines represent roads.

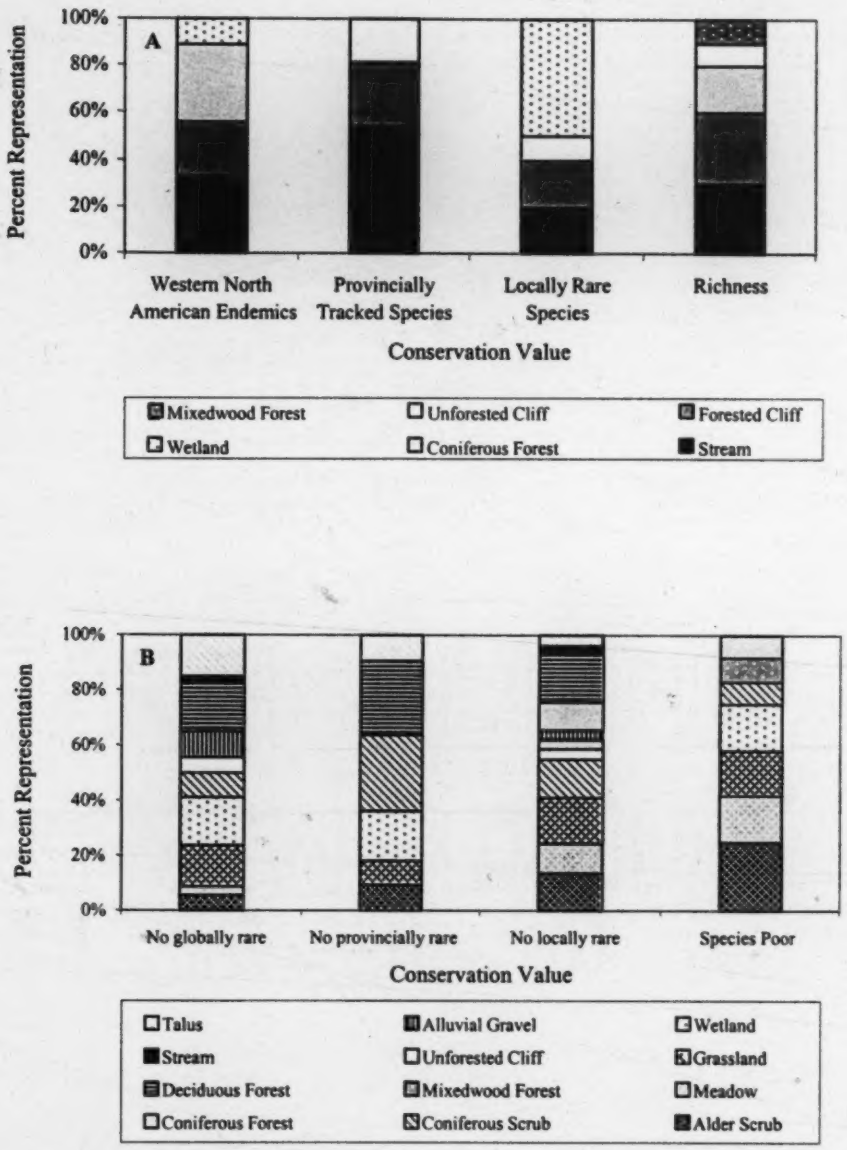


Figure 3.3. Distribution of habitat types among A. moss conservation hotspots and B. coldspots in Waterton Lakes National Park. Bar shading, from top to bottom, is listed in columns, left to right, in the figure legends.

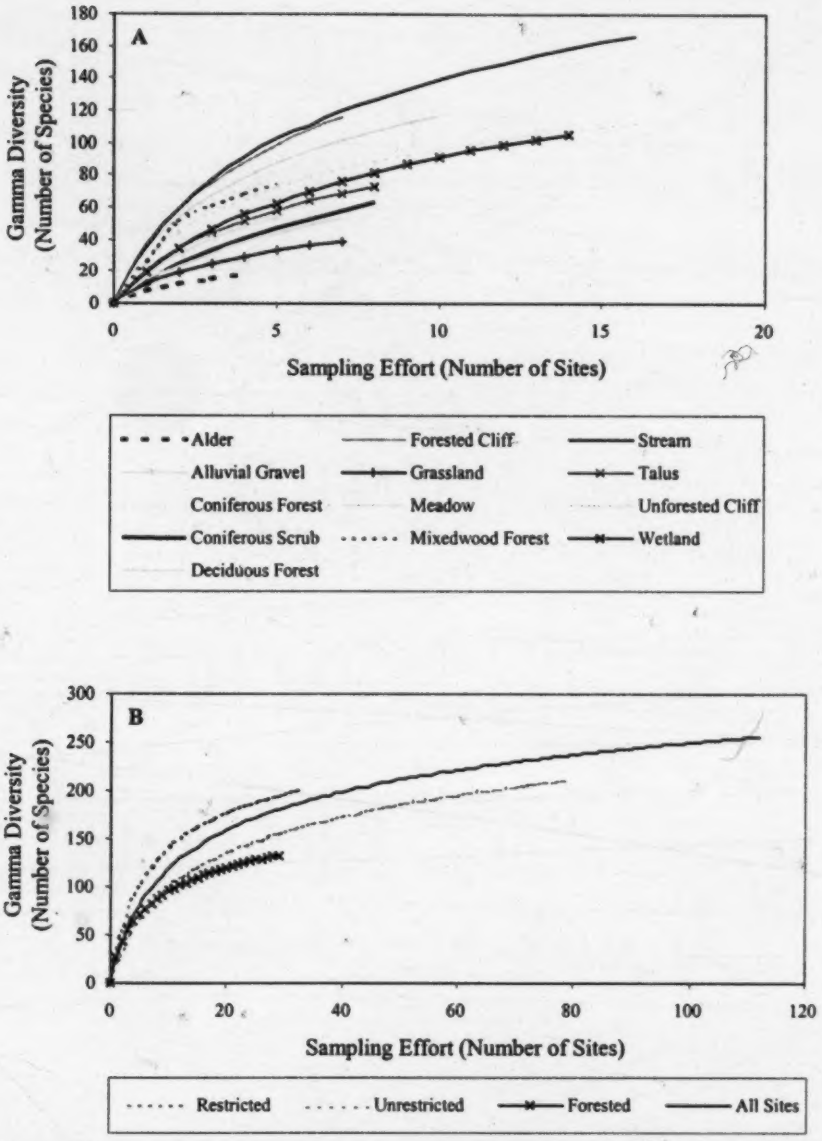


Figure 3.4. Moss species richness (gamma diversity) / sampling effort curves for A. each habitat type, and B. four groups of habitat types sampled in Waterton Lakes National Park.

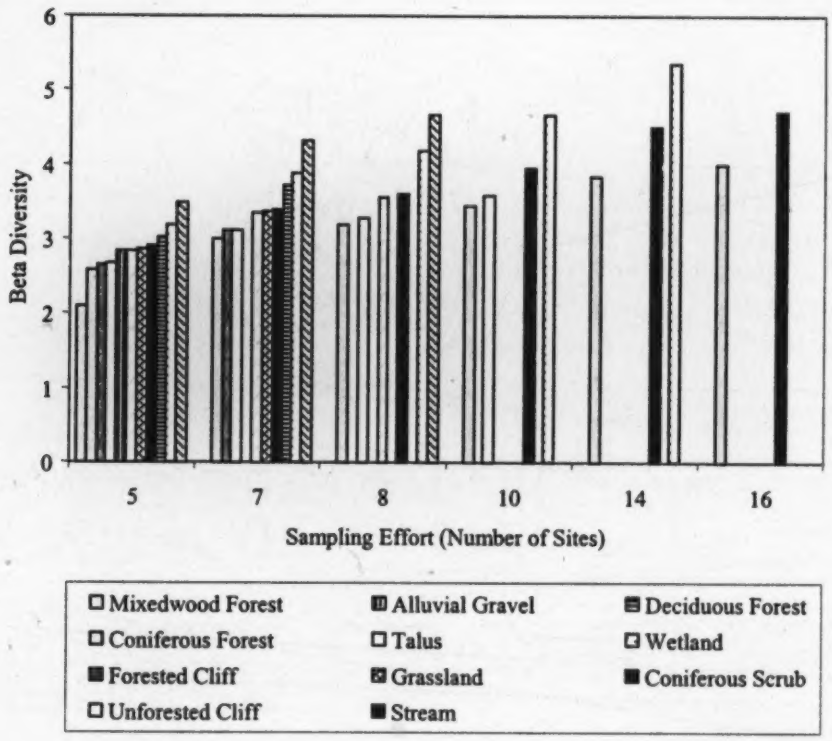


Figure 3.5. Estimated moss beta diversity of each habitat type sampled in Waterton Lakes National Park at different estimated gamma diversities corresponding to different sampling efforts.

Figure 3.6.A. TWINSPAN dendrograms showing classification of moss communities (named after indicator or preferential species) from All sites. Symbols correspond to site types as identified visually for sampling purposes (see legend). Numbers denote eigenvalues at each division. Indicator species are listed at each division, and community names are given at the bottom. Selected preferential species for each community are listed below.

▲ Coniferous Forest
◆ Mixedwood
● Deciduous Forest
▼ Wetland / Shore
★ Coniferous Scrub
○ Grassland / Savannah
☆ Alluvial Gravel
△ Talus
◇ Meadow
▽ Alder Scrub
□ Stream
× Unforested Cliff
+ Forested Cliff

Preferential Species

P. piliferum
Bryum stirtonii
Dicranoweisia crispula
Grimmia montana
Pohlia bolanderi
Polytrichum lyalii

B. velutinum
Brachythecium leibergii
Minum spinulosum
Mnium arizonicum
Orthotrichum alpestre
Tortula mucronifolia

B. erythrorrhizon
Brachythecium nelsonii
Brahcythecium rivulare
Bryum weigelii
Pohlia wahlenbergii
Sphagnum russowii

M. spinulosum
Brachythecium leibergii
Brachythecium reflexum
Mnium spinulosum
Pleurozium schreberi
Orthodicranum strictum

H. aeneum
Encalypta procera
Grimmia anomala
Homalothecium aeneum
Myurella julacea
Pseudoleskieella nervosa

D. aduncus
Brachythecium mildeanum
Leptodictyum riparium
Orthotrichum speciosum
Plagiomnium ellipticum
Pylaisiella polyantha

T. norvegica
Brachythecium albicans
Brachythecium collinum
Desmatodon latifolius
Dicranoweisia crispula
Pohlia cruda

W. controversa
Aulacomnium androgynum
Bryum argenteum
Bryum caespiticium
Polytrichum juniperinum
Weissia controversa

Figure 3.6.A

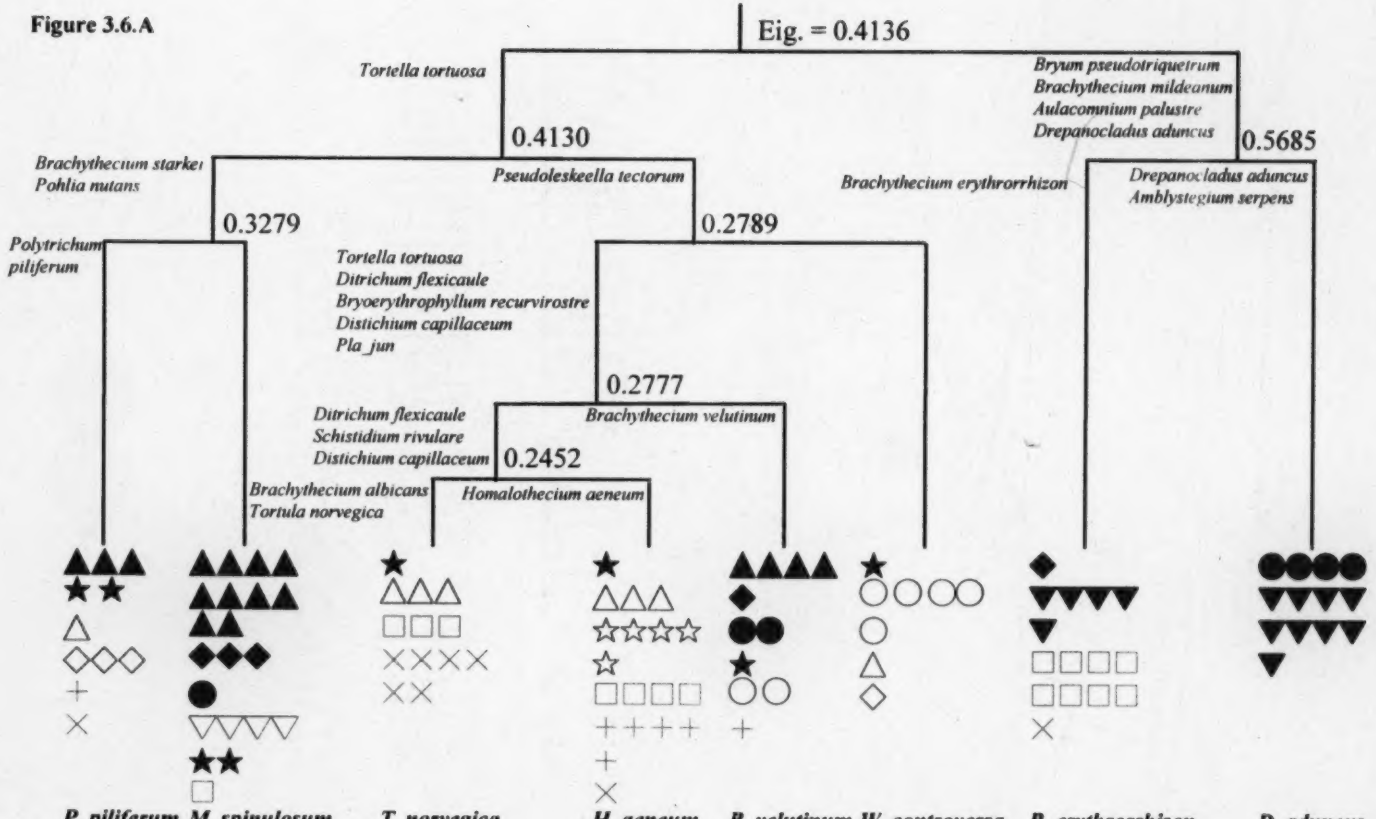

Eig. = 0.4136
Tortella tortuosa
Bryum pseudotriquetrum
Brachythecium mildeanum
Aulacomnium palustre
Drepanocladus aduncus
0.4130
0.5685
Brachythecium starkei
Pohlia nutans
Pseudoleskeella tectorum
Brachythecium erythrorrhizon
Drepanocladus aduncus
Amblystegium serpens
0.3279
0.2789
Polytrichum piliferum
Tortella tortuosa
Ditrichum flexicaule
Bryoerythrophyllum recurvirostre
Distichium capillaceum
Pla_jun
0.2777
Ditrichum flexicaule
Schistidium rivulare
Distichium capillaceum
Brachythecium velutinum
0.2452
Brachythecium albicans
Tortula norvegica
Homalothecium aeneum
P. piliferum
M. spinulosum
T. norvegica
H. aeneum
B. velutinum
W. controversa
B. erythrorrhizon
D. aduncus

Figure 3.6.B. TWINSPAN dendrograms showing classification of moss communities (named after indicator or preferential species) from unrestricted habitat types. Symbols correspond to site types as identified visually for sampling purposes (see legend, Figure 3.6.A). Numbers denote eigenvalues at each division. Indicator species are listed at each division, and community names are given at the bottom. Selected preferential species for each community are listed below.

Preferential Species

P. bolanderi
Bryum caespiticium
Bryum capillare
Grimmia montana
Pohlia cruda
Polytrichum juniperinum

L. radicosa
Hypnum revolutum
Tortella tortuosa
Tortula norvegica

A. serpens
Brachythecium salebrosum
Bryoerythrophyllum recurvirostre
Lescuraea radicosa
Pylaisiella polyantha
Tortula mucronifolia

P. incurvata
Lescuraea stenophylla
Pohlia wahlenbergii
Pseudoleskea incurvata

P. lyallii
Ceratodon purpureus
Grimmia montana
Polytrichum lyallii
Polytrichum piliferum

B. hylotapetum
Brachythecium erythrorrhizon
Eurhynchium pulchellum
Mnium spinulosum
Orthodicranum strictum
Pleurozium schreberi
Rhytidiopsis robusta

D. aduncus
Amblystegium serpens
Aulacomnium palustre
Brachythecium mildeanum
Leptobryum pyriforme
Plagiomnium ellipticum
Pylaisiella polyantha

Figure 3.6.B

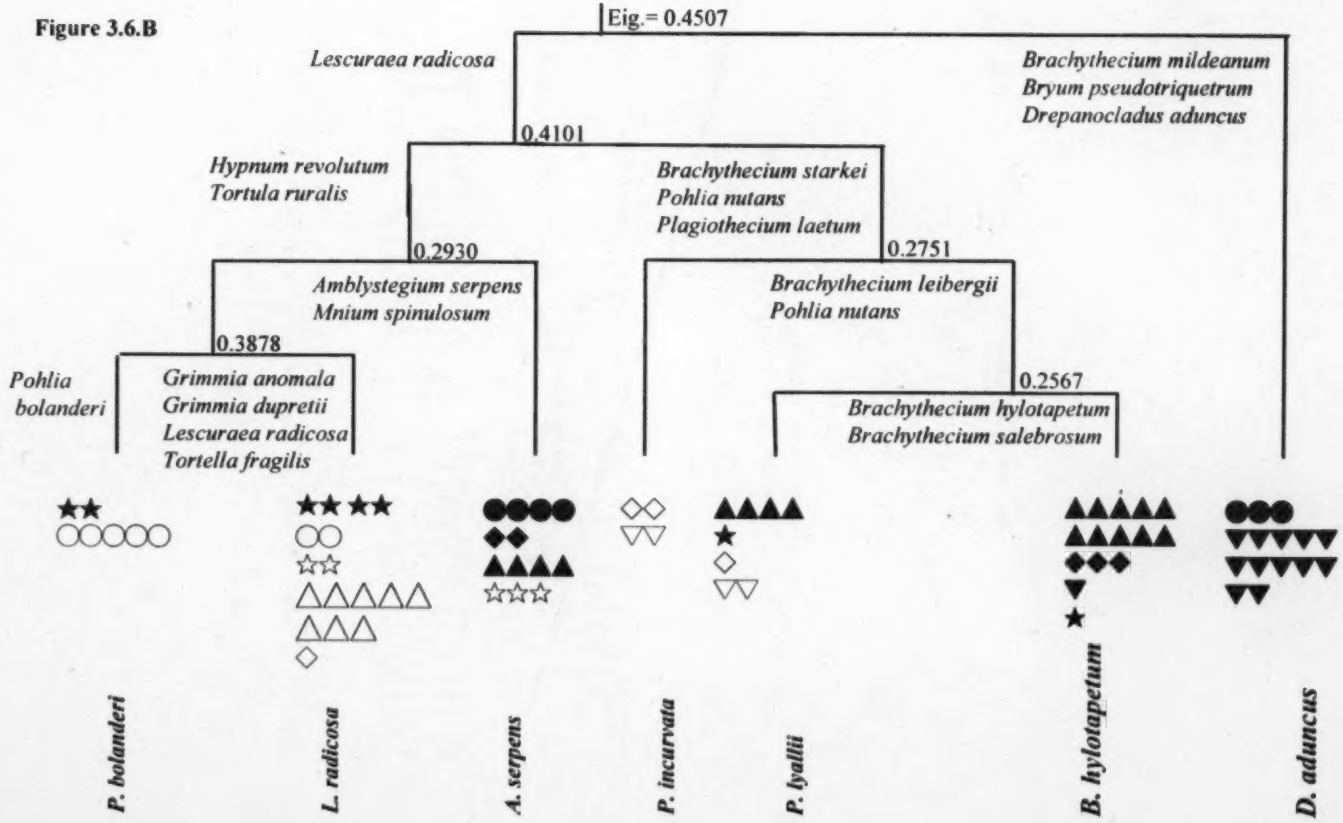
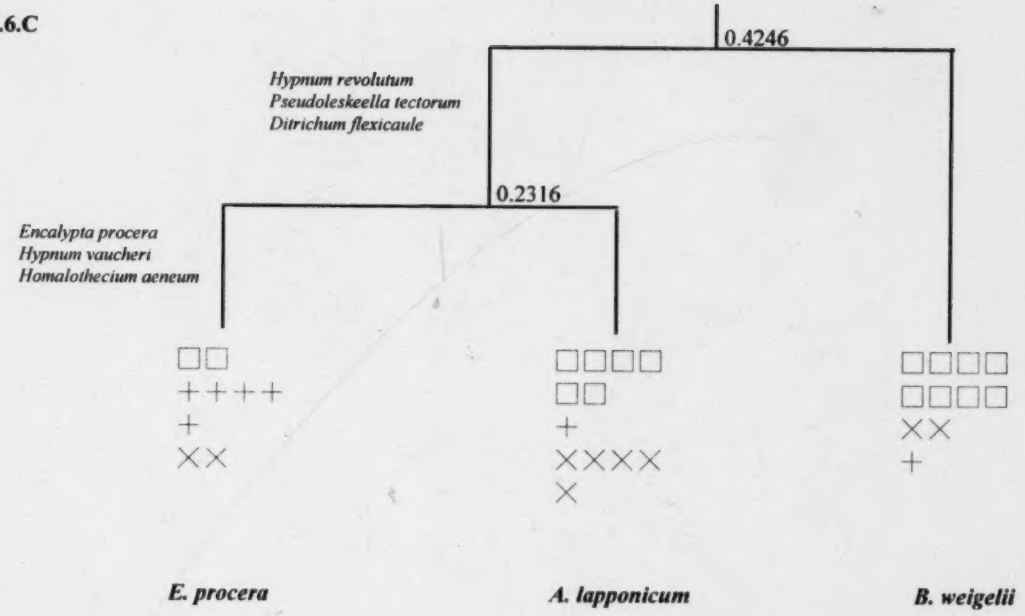

Eig.= 0.4507
Lescuraea radicosa
Brachythecium mildeanum
Bryum pseudotriquetrum
Drepanocladus aduncus
0.4101
Hypnum revolutum
Tortula ruralis
Brachythecium starkei
Pohlia nutans
Plagiothecium laetum
0.2930
0.2751
Amblystegium serpens
Mnium spinulosum
Brachythecium leibergii
Pohlia nutans
0.3878
0.2567
Pohlia bolanderi
Grimmia anomala
Grimmia dupretii
Lescuraea radicosa
Tortella fragilis
Brachythecium hylotapetum
Brachythecium salebrosum
P. bolanderi
L. radicosa
A. serpens
P. incurvata
P. lyallii
B. hylotapetum
D. aduncus

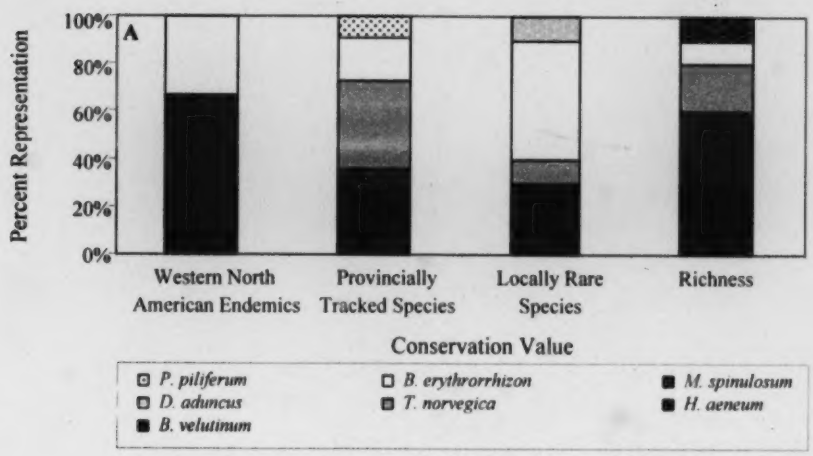
Figure 3.6.C. TWINSPAN dendrograms showing classification of moss communities (named after indicator or preferential species) fromrestricted habitat types. Symbols correspond to site types as identified visually for sampling purposes (see legend Figure 3.6.A). Numbers denote eigenvalues at each division. Indicator species are listed at each division, and community names are given at the bottom. Selected preferential species for each community are listed below.

Preferential Species

E. procera	***A. lapponicum***	***B. weigelii***
Bryum capillare	*Amphidium lapponicum*	*Brachythecium nelsonii*
Encalypta rhaptocarpa	*Lescuraea radicosa*	*Bryum weigelii*
Grimmia anomala	*Pohlia cruda*	*Hygrohypnum ochraceum*
Myurella julacea	*Philonotis fontana*	*Mnium blytii*
Orthotrichum laevigatum	*Tortula norvegica*	*Pohlia wahelnbergii*

Figure 3.6.C


0.4246
Hypnum revolutum
Pseudoleskeella tectorum
Ditrichum flexicaule
0.2316
Encalypta procera
Hypnum vaucheri
Homalothecium aeneum
E. procera
A. lapponicum
B. weigelii



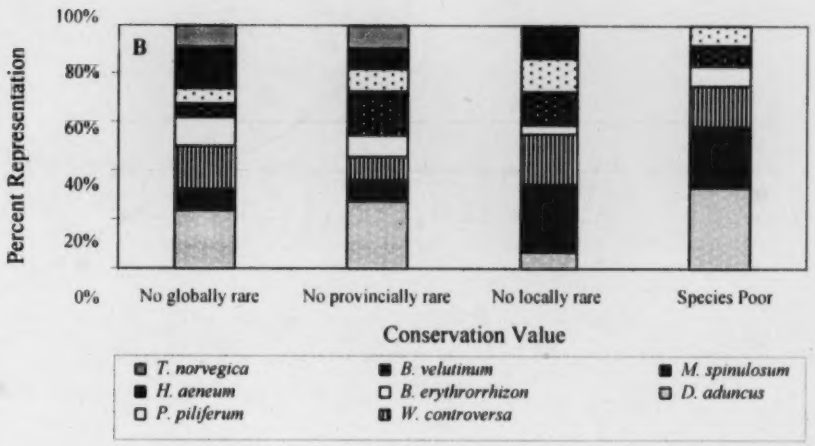


Figure 3.7. Distribution of moss community types (full dataset) among A. moss conservation hotspots and B. coldspots

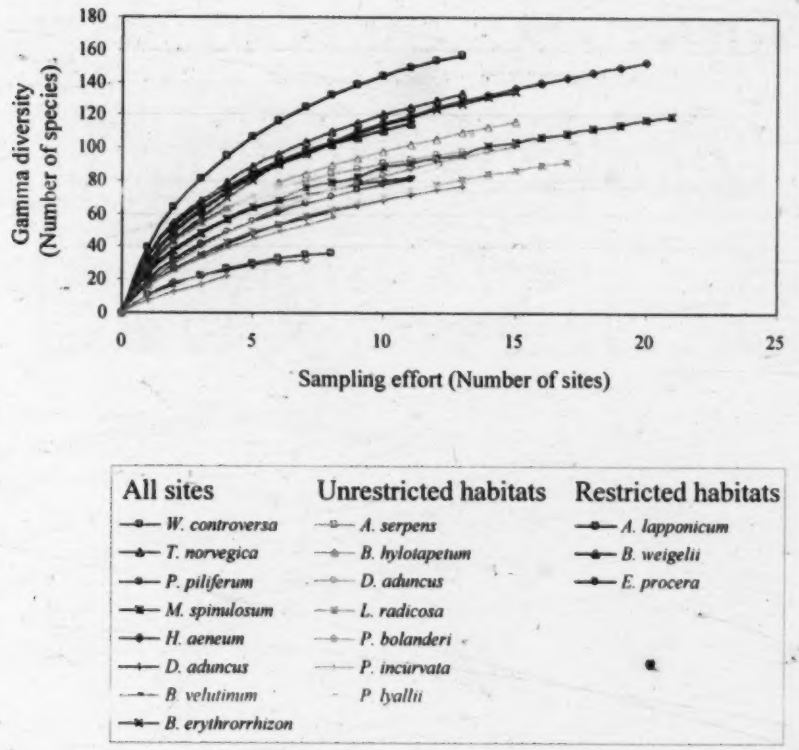
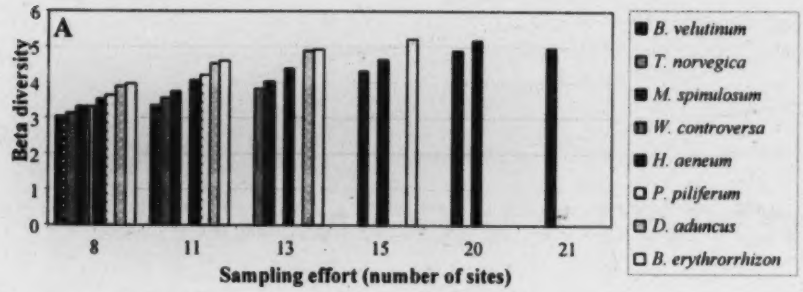
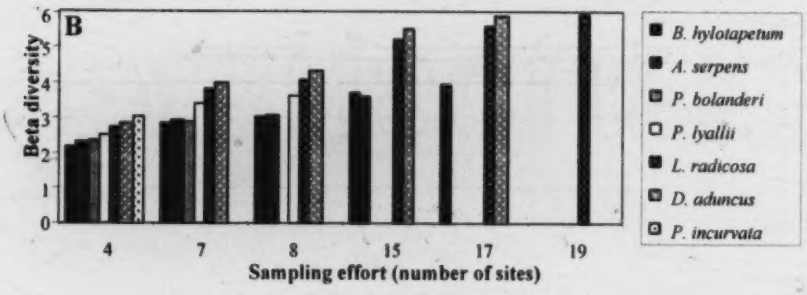


Figure 3.8. Moss species richness (gamma diversity) / sampling effort curves TWINSPAN communities (site groups) in Waterton Lakes National Park. Communities are named for indicator or preferential species, defined by TWINSPAN (Figure 3.6).





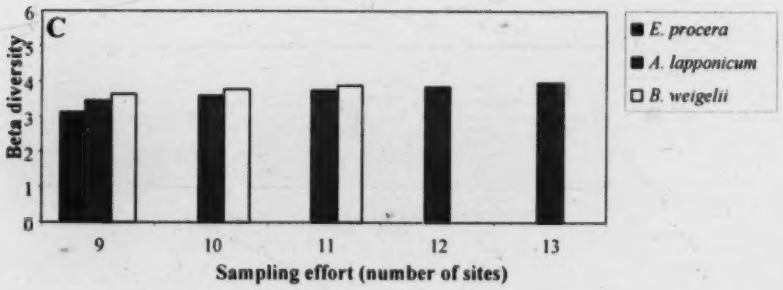


Figure 3.9. Estimated moss beta diversity of each TWINSPAN community in Waterton Lakes National Park at different estimated gamma diversities corresponding to different sampling efforts. Communities resulted from the classification of A. All sites, B. Unrestricted habitats, and C. Restricted habitats.

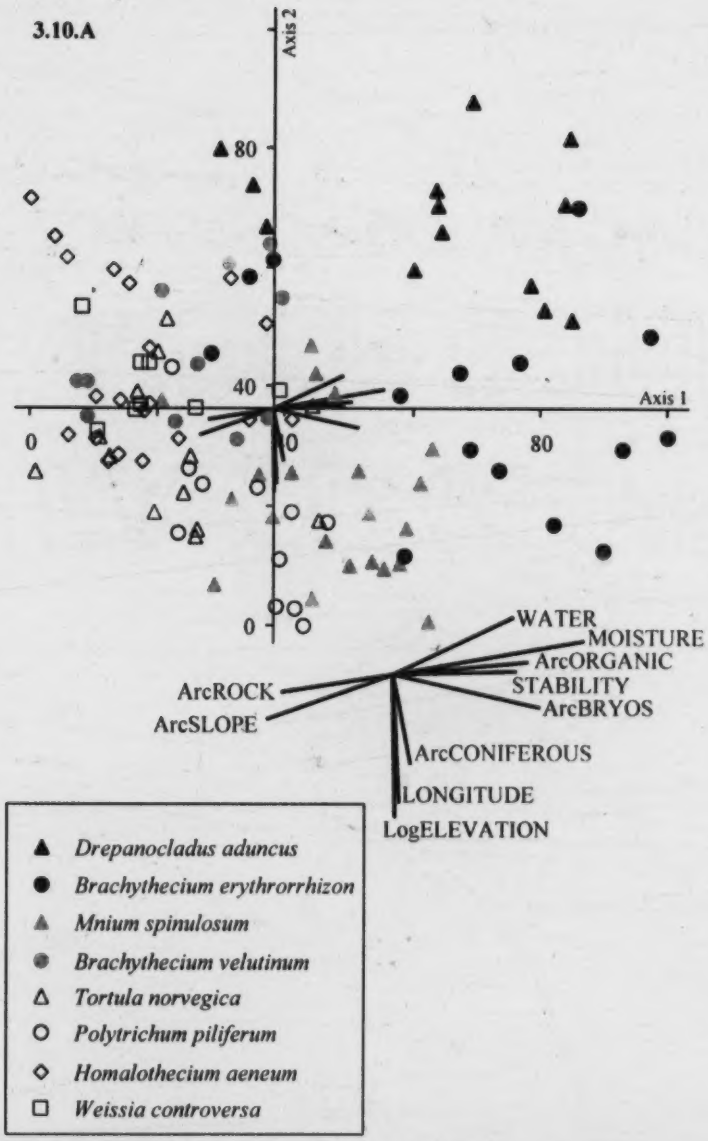
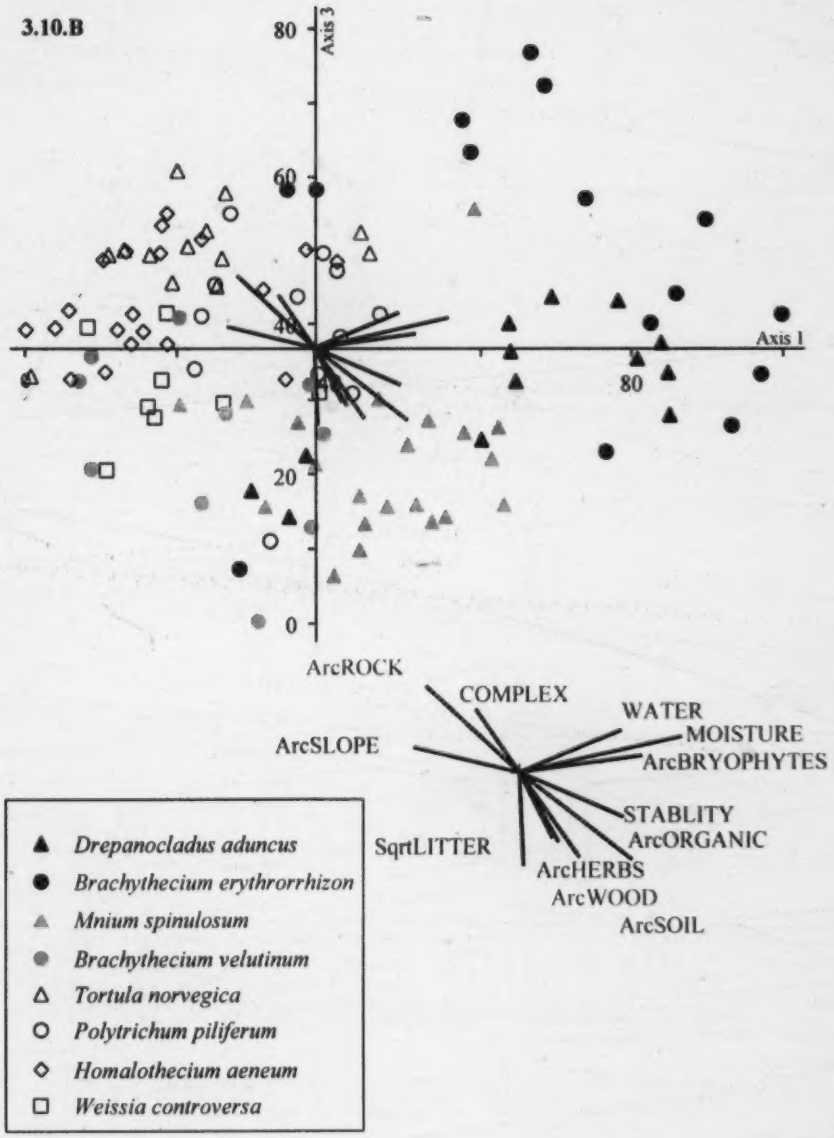
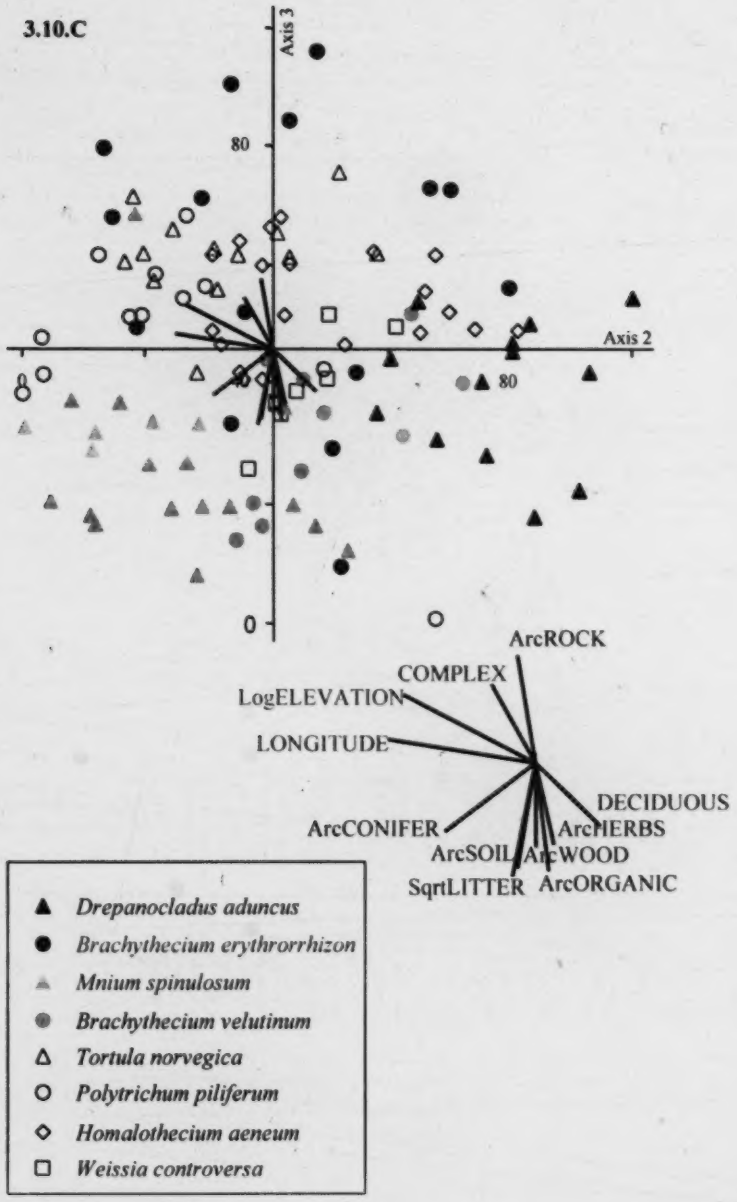
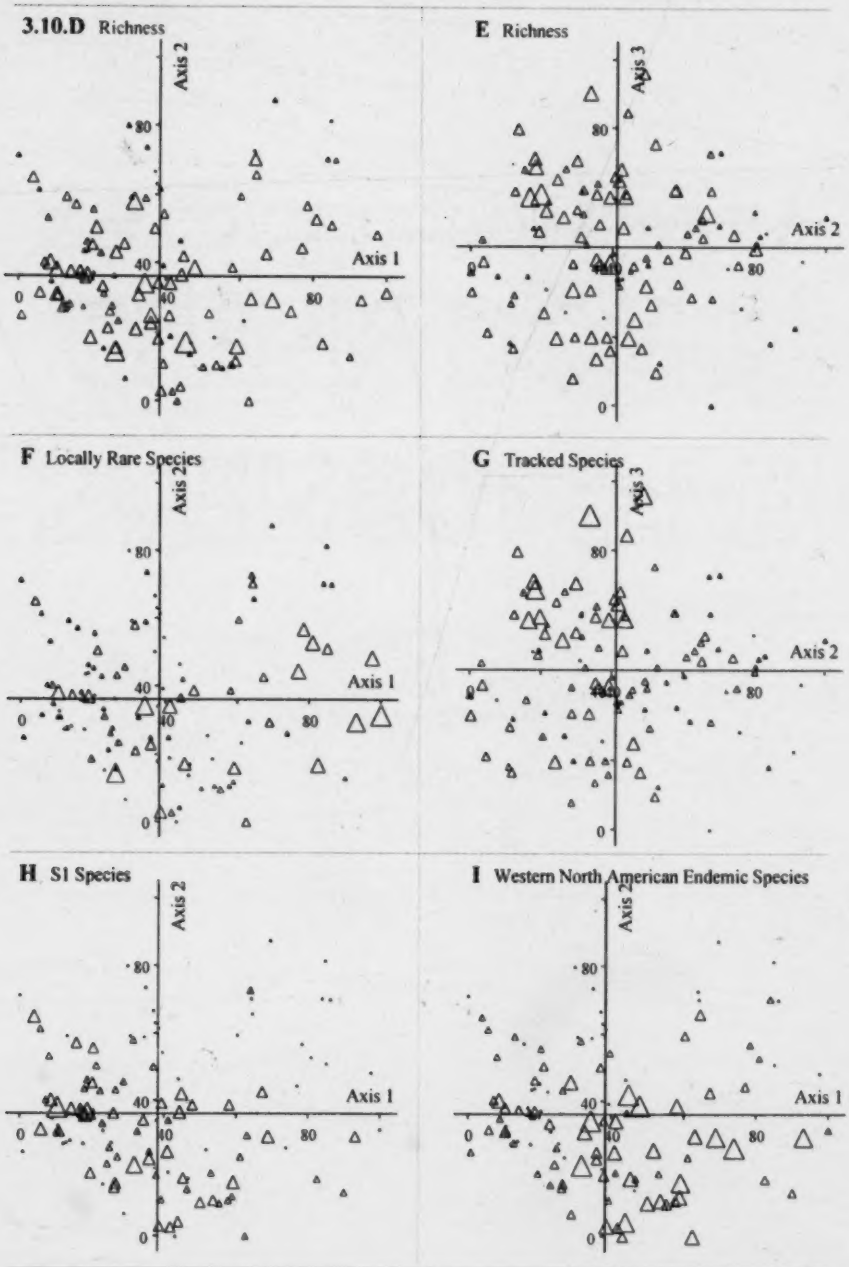


Figure 3.10. Canonical correspondence analysis ordination of all 112 Waterton Lakes National Park sites overlaid with A.-C. TWINSPAN communities, D.-E. species richness, F. number of locally rare species, G. number of provincially tracked species, H. number of S1 (one to five provincial occurrences) species, and I. number of western North American endemic species. Variable names follow Table 3.2, with prefixes "Arc", "Sqrt", and "Log" indicating arcsine, square root, and log transformations respectively.


3.10.B
Axis 3
Axis 1
80
60
40
20
0
80
ArcROCK
COMPLEX
WATER
MOISTURE
ArcSLOPE
ArcBRYOPHYTES
STABLITY
ArcORGANIC
SqrtLITTER
ArcHERBS
ArcWOOD
ArcSOIL
Drepanocladus aduncus
Brachythecium erythrorrhizon
Mnium spinulosum
Brachythecium velutinum
Tortula norvegica
Polytrichum piliferum
Homalothecium aeneum
Weissia controversa


3.10.C
Axis 3
80
Axis 2
80
0
ArcROCK
COMPLEX
LogELEVATION
LONGITUDE
DECIDUOUS
ArcCONIFER
ArcHERBS
ArcSOIL
ArcWOOD
SqrtLITTER
ArcORGANIC
Drepanocladus aduncus
Brachythecium erythrorrhizon
Mnium spinulosum
Brachythecium velutinum
Tortula norvegica
Polytrichum piliferum
Homalothecium aeneum
Weissia controversa


3.10.D Richness
Axis 2
Axis 1
E Richness
Axis 3
Axis 2
F Locally Rare Species
Axis 2
Axis 1
G Tracked Species
Axis 3
Axis 2
H S1 Species
Axis 2
Axis 1
I Western North American Endemic Species
Axis 2
Axis 1
0
40
80

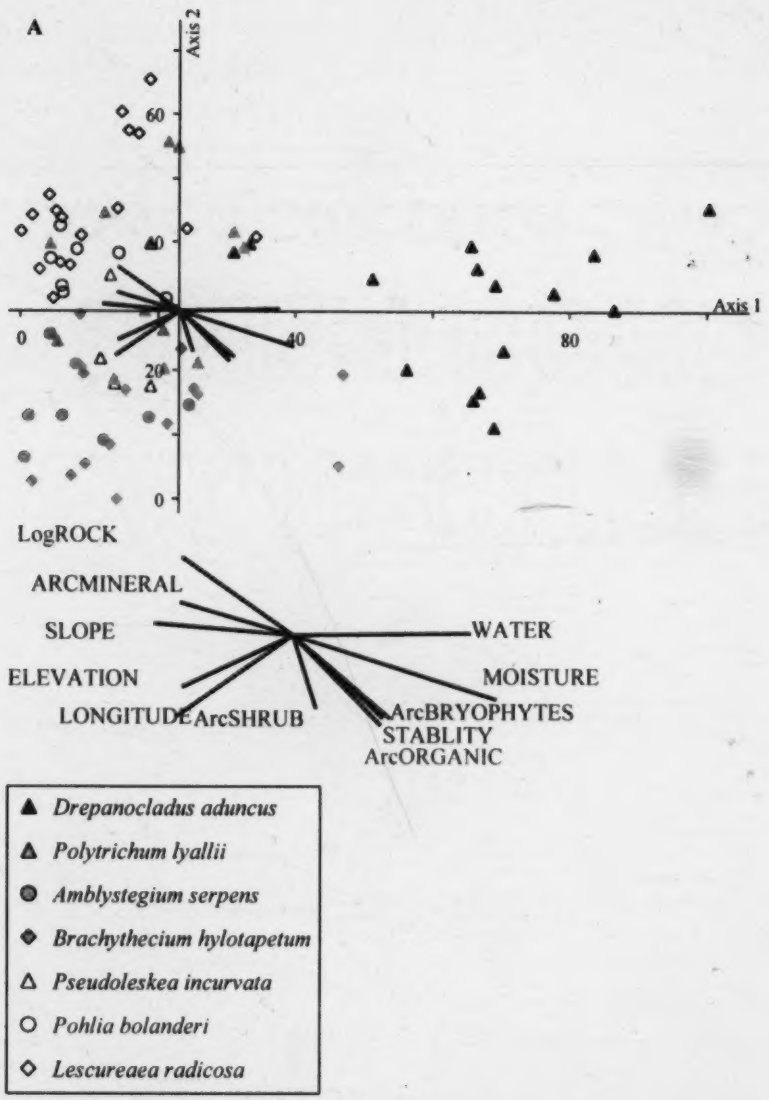


Figure 3.11. Canonical correspondence analysis ordination of 79 unrestricted habitats in Waterton Lakes National Park sites overlaid with A. TWINSPAN communities, B.-C. species richness, D. number of locally rare species, E. number of provincially tracked species, F. number of S1 species, and G. number of western North American endemic species. Variable names follow Table 3.2, with prefixes "Arc", "Sqrt", and "Log" indicating arcsine, square root, and log transformations respectively.

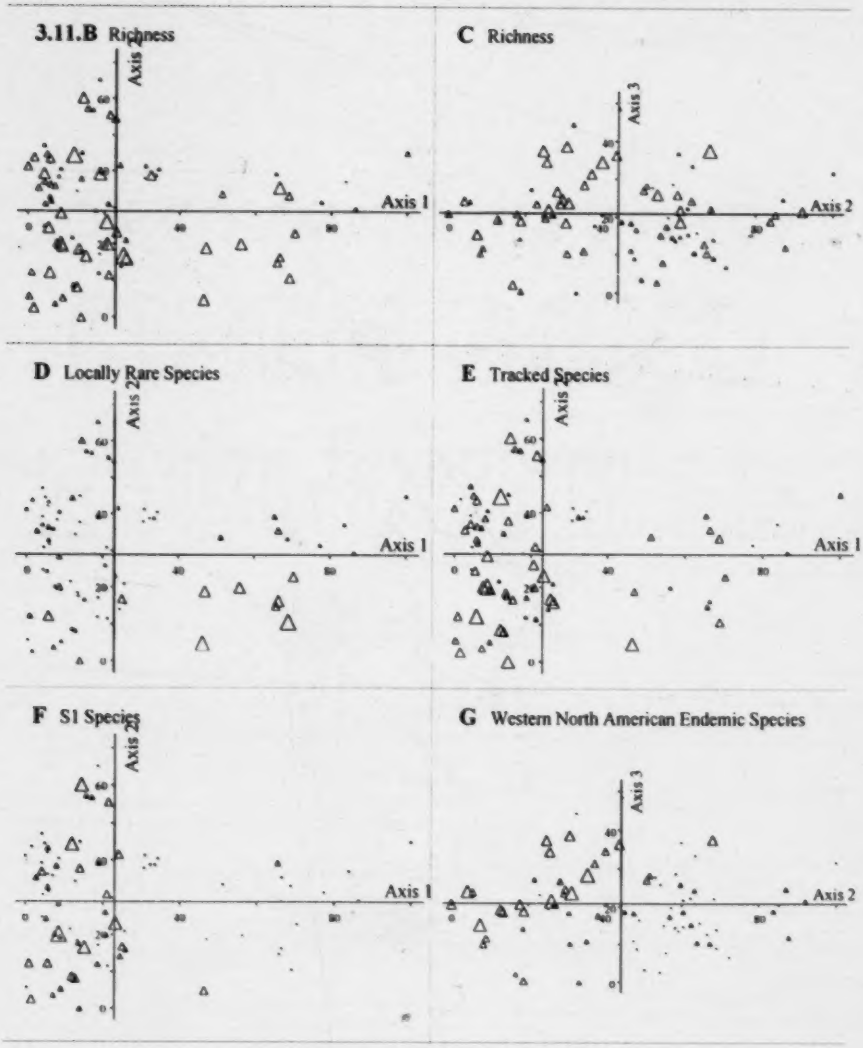
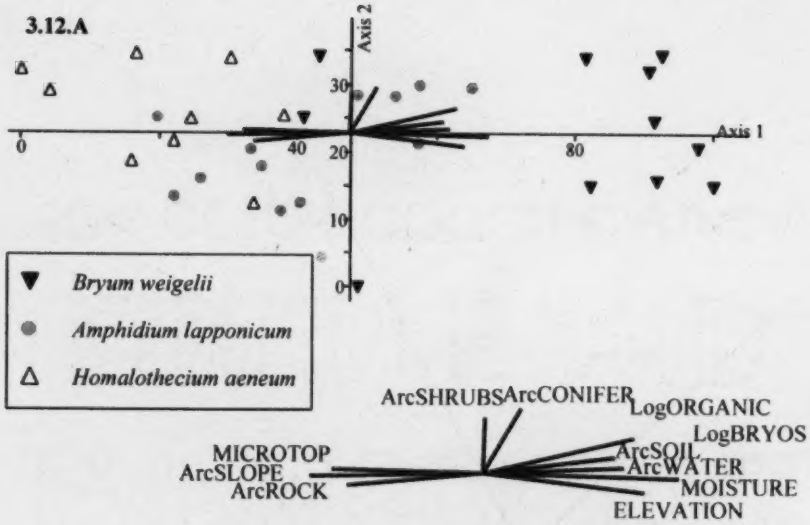
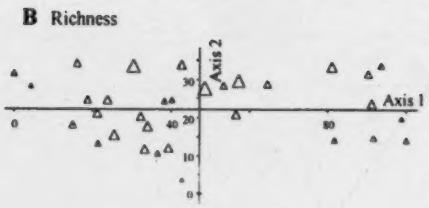
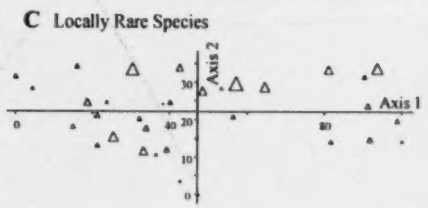
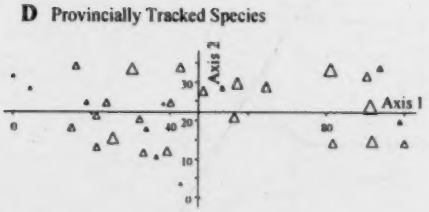

3.11.B Richness
Axis 2
Axis 1
C Richness
Axis 3
Axis 2
D Locally Rare Species
Axis 2
Axis 1
E Tracked Species
Axis 2
Axis 1
F S1 Species
Axis 2
Axis 1
G Western North American Endemic Species
Axis 3
Axis 2

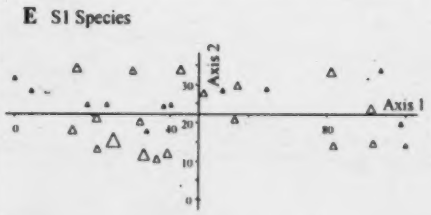
Figure 3.12. Canonical correspondence analysis ordination of 33 restricted habitats in Waterton Lakes National Park sites overlaid with A. TWINSPAN communities, B. species richness, C. number of locally rare species, D. number of provincially tracked species, E. number of S1 species, and F. number of western North American endemic species. Variable names follow Table 3.2, with prefixes "Arc", "Sqrt", and "Log" indicating arcsine, square root, and log transformations respectively.


3.12.A
Axis 2
Axis 1
0
40
20
80
30
10
0
Bryum weigelii
Amphidium lapponicum
Homalothecium aeneum
ArcSHRUBS
ArcCONIFER
LogORGANIC
LogBRYOS
ArcSOIL
ArcWATER
MOISTURE
ELEVATION
MICROTOP
ArcSLOPE
ArcROCK


B Richness
Axis 2
Axis 1


C Locally Rare Species
Axis 2
Axis 1


D Provincially Tracked Species
Axis 2
Axis 1


E S1 Species
Axis 2
Axis 1

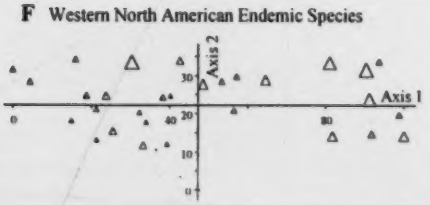
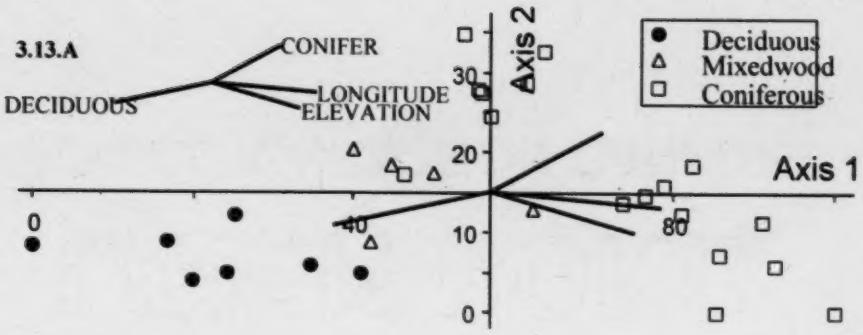
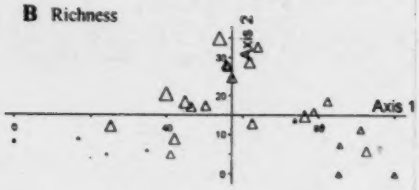

F Western North American Endemic Species
Axis 2
Axis 1

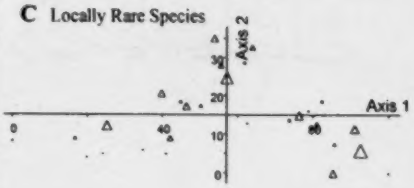
Figure 3.13. Canonical correspondence analysis ordination of 29 forested sites Waterton Lakes National Park sites overlaid with A. habitat type, B. species richness, C. number of locally rare species, D. number of provincially tracked species, E. number of S1 species, and F. number of western North American endemic species. Variable names follow Table 3.2.



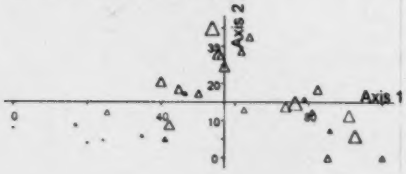
B Richness



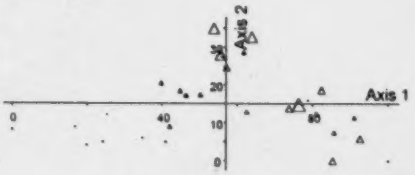
C Locally Rare Species



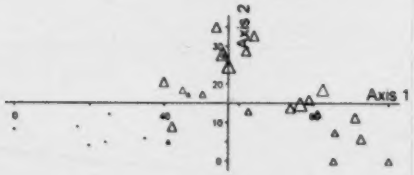
D Provincially Tracked Species



E S1 Species



F Western North American Endemic Species



4. CONCLUSION

This study explores plant inventory data at several scales and in several ways to maximize its utility to the managers of the park from which the data were gathered. While important management implications are drawn from the analyses, many more analyses may be conducted with this data to benefit the understanding of patterns of conservation value in parks. New studies are also suggested by the conclusions of the present work.

4.1 The importance of scale in floristic and ecological analysis for management application

It is crucial for scientists developing management recommendations and for managers applying them to consider different scales of study and management in their respective work. Scientists, for example, may make their work more applicable to conservation efforts by implementing sampling schemes on the scale of a region being managed and of management activities within it. Managers, for their part, may increase the value of management decisions by recognizing the scales of rarity and diversity greater and smaller than their jurisdiction when establishing conservation priorities and strategies. Furthermore, they must recognize and attempt to compensate for potential discrepancies between the scale on which research was conducted and the scale of management activities. Different scales of study reveal different patterns and address different management needs. The simultaneous consideration of multiple scales can improve both scientific understanding and management efficiency: ecological relationships at a given scale are better understood within the context of scales encompassed by and encompassing them (Bunnell & Huggard 1999).

Bunnell and Huggard (1999) note that in considering species diversity of many taxa, the scale appropriate for study is not necessarily the scale at which management actions are applied. With this problem in mind, the goal of drawing management implications from the data directed the sampling approach used in this study. Park managers use zones and sites to manage human use. Stohlgren et al. (1997) confirm that most park management decisions are made locally, and encourage researchers to avoid underestimation of species richness and resultant poor predictive ability of predictive models based on coarse sampling across large areas. Gould and Walker (1999) and Heikkinen (1998) point out that most patterns of rare species distribution are documented at small or large scales, but that few researchers

address the more conservation-appropriate 'meso-scale'. For the current study, microhabitat preferences of moss species are probably of most importance in determining moss species distribution (e.g. Geissler 1982), and a more rewarding project from a research standpoint may have focussed on the distribution of moss species with respect to microhabitats in a single habitat type. However, this would have limited the utility of the research to managers who must protect many species across a park composed of many habitat types by managing human use on a strictly human scale.

The current study deals with bryophyte diversity and rarity on the scale of parks in a region and of habitats in a park, both of which are relevant to park management. *Within the northern Rocky Mountains*, the distribution of bryophytes is important because the positions of local range limits and pockets of diversity or endemism help to establish the conservation value of a particular region compared with others. This information can help managers to define conservation management priorities. For example, an exceptionally high proportion of the moss flora of Waterton Lakes National Park is endemic to western North America (chapter 2). Although nearby sites in British Columbia and Montana also support many endemic species, high representation by these species makes Waterton unique within the jurisdiction of Alberta. Furthermore, many of Waterton's western North American endemics are at their eastern range limits in Canada (chapter 2). Given that National Parks aim to preserve Canada's biodiversity, then, the preservation of western North American endemics may be assigned high management priority.

Within Waterton Lakes National Park, the distribution of conservation value is key to patterning park management activities. If managers give high priority to preserving western North American endemics, for example, they need to know the locations of these species within park boundaries. This information allows them to protect endemic species by directing human disturbance to areas with fewer endemics, or by maintaining natural, ecological processes characteristic of sites with high numbers of endemic species. Inventory data provides specific locations for endemic species. More importantly, however, it allows researchers to relate the richness of endemic species to environmental and geographical gradients so that the occurrence of western North American endemics can be predicted in uninventoried areas. In this study, high elevation coniferous forest sites, particularly those in the west part of the park, tended to support greater numbers of western North American Endemics (chapter 3). The potential value

of these kinds of sites should be taken into consideration when new inventory work is done, or when sites are being evaluated for human use or protection.

The search for environmental cues to the occurrence of moss richness and rare moss species for management application requires consideration of scale and complexity in other respects as well. Management applications require simplicity, whereas the natural areas being managed are infinitely complex. As noted above, for example, managers require a more coarse scale for management, but a fine scale is perhaps more relevant to the ecology of the species of interest. The most reliable way of determining patterns of conservation value in Waterton would be to inventory the entire park, whereas budgetary considerations require that conservation value be measured in a few places, and predicted in most places. Diversity and rarity, values prized by parks and researchers alike, result from a complex array of specific environmental, historical, and genetic cases, yet the prediction of conservation value requires the derivation and application of a general rule. Nature varies continuously whereas human applications require that natural areas be divided into simplified, discrete units – such as sites, habitats, communities, and parks. Many taxa are essential to ecosystem function, yet we base management decisions on only a few. Finding adequate compromises requires careful thought and discussion.

To this end, it should be remembered that the distribution of conservation value in Waterton Lakes National Park is more complex than the management recommendations arising from this study may suggest. Continued research is required. While implementing these recommendations, managers should solicit further research and information. Management strategy, in turn, must remain dynamic, and current with accumulating knowledge (Bunnell & Huggard 1999).

4.2 The need for bryophyte inventories and their thorough interpretation

Inventory work and its thorough exploitation, are especially important in view of the rapid change characteristic of our natural world. Industrial, urban, and natural resource development outside of protected areas fragments and destroys habitat which may otherwise support high diversity or other conservation value, placing a greater onus on parks to preserve species and their habitats and at the same time driving people into parks for recreational escape. The importance of inventories and analyses that facilitate and

expedite informed management and provide baseline data against which future incarnations of parks can be compared cannot be overemphasized.

Furthermore, global climate change is expected to have significant effects on mountain habitats. Vegetation zones may migrate 400-600m upslope (Nilsson & Pitt 1991 in Grabherr et al. 1995), and the encroachment of subalpine forest may threaten alpine tundra (Boer et al. 1990 in Grabherr et al. 1995) in the Rockies. The elimination of entire vegetation zones may drastically reduce biodiversity (Grabherr et al. 1995). At the same time, Grabherr et al. (1995) point out that mountain habitats also tend to provide microhabitats in which plants can survive despite overall climatic unfavourability, which may prove to be a boon to species migrating slowly with respect to altitude or latitude. Mountain parks are especially significant in view of these possibilities.

Climate change, furthermore, has the power to dramatically alter the climatic conditions that may allow species to occupy distributional outposts (Parks Canada 2000). Many species in Waterton Lakes National Park are currently at the edge of their distributional range. An understanding of diversity patterns with respect to environment may help us understand how climate change may affect diversity in the future. Grabherr et al. (1995) also speculate that different habitat types will be affected by climate change at different rates, and point out that predictions of future diversity will have to account for the varying contribution of different habitat types to diversity (chapter 3) in addition to their different vulnerabilities.

The sensitivity of taxa such as non-vascular plants and lichens to environmental change adds to the urgency of drawing these species into management consideration. Bryophytes and lichens respond to and accumulate atmospheric pollutants in the wild, and thus make excellent biomonitors of impurities that may be affecting the ecosystem as a whole (e.g. Puckett 1988; Rao et al. 1977; Tyler 1990). Although the Waterton management plan proposes the use of several specific animal taxa as indicators of ecosystem integrity, plant diversity is not proposed. Despite stated priorities of biodiversity conservation and monitoring for environmental change (including air quality), no specific mention of non-vascular plants is made.

4.3 Further research

4.3.1 New scales

The micro-scale (within individual Waterton sites) is not addressed in this study, and may be particularly important in determining patterns of moss conservation value. Determining patterns of bryophyte occurrence within microhabitats is confounded by several factors, including the diverse array of microhabitats available for sampling. Microhabitats are almost as diverse as the species themselves, with potentially infinite combinations of features (rock chemistry, texture, setting, etc.) which may be of predictive importance. However, microhabitat features do appear to be key to the occurrence of certain bryophyte species and types of species (e.g. Kruys et al. 1999, Muhle & LeBlanc 1975, Newmaster 2000, Rambo & Muir 1998, Vitt et al. 1995), and they have potential to considerably improve the predictive power of models based on site features.

4.3.2 New approaches

Further work with Waterton data, now in progress, attempts to model conservation value with respect to environmental variables directly through generalized linear regression. Regression models have been sucessfully developed for rare species and species richness at several scales, for several types of plants (e.g. Gould & Walker 1999; Heikkinen 1998; Hill & Keddy 1992; McIntyre & Lavorel 1994; Miller 1986; White & Miller 1988).

In this study, patterns of moss conservation value were examined with respect environmental and compositional gradients using canonical correspondence analysis. Correlating conservation value with ordination axes representing combinations of variables has the advantages of visualizing complex relationships and of exploring many environmental and compositional variables at once. However, these correlations also depend on a close relationship between species composition and conservation value. Mosses are good indicators of their immediate environment, and many recurring variables explaining change in conservation value – disturbance, climate, edaphic factors, for example – are known to be important to moss species composition. Habitat heterogeneity, another well-documented correlate of species richness (e.g. Gould & Walker 1999; La Roi & Stringer 1975; Newmaster 2000; Vitt et al. 1995), on the other hand, promotes conservation value by supporting a *variety* of species and is not related to

specific ecological preferences. By determining predictive relationships between explanatory variables and conservation value directly, the correlation of conservation value and species composition is circumvented.

In conjuction with the building of regression models defining relationships between environmental variables and conservation value, the same variables are being investigated through variance paritioning in canoncial correspondence analysis (Borcard et al. 1992; Økland & Eilertsen 1994) for their individual and combined roles in explaining variation in species composition. Variables important for species composition can be compared with variables explaining conservation value to clarify mechanisms through which conservation value is predicted: Are variables explaining conservation value important because of their effect on species ecology or do they strictly influence species number? Might the strength or weakness of a predictive relationship reflect the degree of ecological relevance a variable has to a given group of species? Furthermore, even though many permutations of species composition result in numerically equivalent conservation values, it is often desirable to preserve the compositional character of sites within a park. The preservation of moss community differentiation depends on the maintenance of factors contributing to patterns of species composition.

4.3.3 New regions

The approaches used in this study may be applied in new regions to allow floristic comparisons between more parks and to add to our understanding of how diversity and rarity can be best managed. The eventual coalescence of areas in which this type of study has been completed would allow for exciting analyses at many, nested scales, and would provide a sound base from which management activities in different parks could be co-ordinated.

4.4 Conclusion

This study shows that inventory data may be successfully explored for patterns of distribution of conservation value (high richness, high numbers of rare species) that can be directly applied by park managers to prioritize and conserve species and species diversity. These techniques are particularly valuable for the management of species (such as mosses) that are difficult to find and identify, which attract little funding and have traditionally received little management attention. The thorough analysis of

inventory data reveals the locations of sites of high management priority, and, more importantly, helps to indicate where high conservation value is likely to occur in the uninventoried majority of a park. While these predictions oversimplify the complexity of diversity and rare species distribution, they provide a starting point from which species that are currently neglected in management plans can be incorporated into management activities. The maintenance of dynamic management plans will allow the incorporation of improved predictions as increased sampling and improved inventory techniques contribute new data, as resources permit.

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Appendix A. List of moss species in each of six Rocky Mountain regions with their climatic affinities (A=Arctic-Alpine, B=Boreal, C=Cosmopolitan, M=Montane, T=Temperate) and generalized world distributions (A=Arctic-Alpine, D=Disjunct, E=Endemic, O=Continuous). Asterisks (*) denote species endemic to western North America.

Species	Phytogeographic Affinity	World Distribtuion	West Slopes	Glacier National Park	Waterton Lakes National Park	Banff National Park	Jasper National Park	Willmore Wilderness Area
Abietinella abietinum	B	O	•	•	•	•	•	•
Aloina brevirostris	B	D				•	•	•
Aloina rigida	T	D					•	
Amblyodon dealbatus	A	A				•	•	•
Amblystegium juratzkanum	C			•	•		•	
Amblystegium serpens	C		•	•	•	•	•	•
Amblystegium varium	T	O			•	•	•	
Amphidium lapponicum	B	O	•	•	•	•	•	•
Amphidium mougeotii	B	D		•				
Andreaea alpestris	M	D					•	
Andreaea blyttii	M	O					•	
Andreaea nivalis	M	O					•	
Andreaea rupestris	B	O	•	•	•	•	•	
Anoectangium aestivum	T	O	•		•		•	
Anomobryum filiforme	B	D			•		•	•
Antitrichia californica	T	D		•				
Antitrichia curtipendula	B	D	•					
Aongstroemia longipes	M	O	•				•	•
Arctoa fulvella	M	O					•	
*Atrichum selwynii**	T	E	•	•	•	•	•	•
Atrichum tenellum	T	O		•				
Atrichum undulatum	B	O	•	•			•	
Aulacomnium acuminatum	A	O					•	•
Aulacomnium androgynum	T	D	•	•	•		•	
Aulacomnium palustre	C		•	•	•	•	•	•
Aulacomnium turgidum	A	A			•	•	•	•
Barbula convoluta	B	O	•	•	•	•	•	
*Barbula eustegia**	M	E			•			
Barbula unguiculata	B	O		•	•			
Bartramia halleriana	T	D					•	
Bartramia ithyphylla	A	A	•	•	•	•	•	•
Bartramia pomiformis	B	O	•	•	•			
Blindia acuta	B	D	•	•	•	•	•	•
Brachythecium acuminatum	T	E					•	
Brachythecium albicans	B	O	•	•	•	•	•	
*Brachythecium asperrimum**	M	E		•	•			
Brachythecium calcareum	B	E	•		•			•
Brachythecium campestre	B	O			•			•

Species	Phytogeographic Affinity	World Distribtuion	West Slopes	Glacier National Park	Waterton Lakes National Park	Banff National Park	Jasper National Park	Willmore Wilderness Area
Brachythecium collinum	B	D	•	•	•	•	•	•
Brachythecium erythrorrhizon	B	D	•	•	•			
*Brachythecium fendleri**	M	E			•			
*Brachythecium frigidum**	T	E	•	•	•	•		
Brachythecium groenlandicum	A	A	•			•	•	•
*Brachythecium holzingeri**	M	E		•	•			
*Brachythecium hylotapetum**	M	E	•	•	•	•		
*Brachythecium leibergii**	M	E	•	•	•	•		•
Brachythecium mildeanum	B	O			•			
*Brachythecium nelsonii**	M	E	•	•	•	•	•	•
Brachythecium oedipodium	B	O	•	•	•	•	•	•
Brachythecium plumosum	C		•		•			•
Brachythecium populeum	B	O	•					
Brachythecium reflexum	B	O	•		•	•	•	
Brachythecium rivulare	B	O	•	•	•	•	•	•
Brachythecium rutabulum	B	O			•		•	
Brachythecium salebrosum	B	O	•	•	•	•	•	•
Brachythecium turgidum	A	A	•	•	•	•	•	•
Brachythecium velutinum	B	O	•	•	•	•	•	•
Bryobrittonia longipes	A	O					•	•
Bryoerythrophyllum ferruginascens	M	D	•				•	
Bryoerythrophyllum recurvirostre	C		•	•	•	•	•	•
Bryum algovicum	B	O		•	•	•	•	•
Bryum amblyodon	B	O			•	•	•	
Bryum arcticum	B	O		•				
Bryum argenteum	C			•	•	•	•	•
Bryum caespiticium	C		•	•	•	•	•	
*Bryum calobryoides**	M	E			•		•	
Bryum calophyllum	B	O					•	
Bryum capillare	C		•	•	•	•	•	•
Bryum cyclophyllum	B	O	•	•	•			
Bryum flaccidum	U	U					•	•
Bryum gemmiparum	T	D	•	•				
Bryum knowltonii	B	O						•
Bryum lisae var. *cuspidatum*	B	O	•	•	•	•	•	
Bryum subapiculatum	T	D	•					
Bryum miniatum	T	D			•			
Bryum muehlenbeckii	B	D		•	•			
Bryum pallens	B	O		•		•	•	
Bryum pallescens	B	O	•	•	•	•	•	
Bryum pseudotriquetrum	B	O	•	•	•	•	•	•
Bryum purpurascens	B	O				•		
Bryum schleicheri	B	D		•				

Species	Phytogeographic Affinity	World Distribution	West Slopes	Glacier National Park	Waterton Lakes National Park	Banff National Park	Jasper National Park	Willmore Wilderness Area
Bryum stirtonii	B	D	•		•	•	•	
Bryum turbinatum	T	O		•		•	•	
Bryum uliginosum	B	O					•	
Bryum weigelii	B	O	•	•	•	•	•	•
Buxbaumia aphylla	T	O		•	•	•	•	•
*Buxbaumia piperi**	B	E		•				
Buxbaumia viridis	T	D			•			
Calliergon cordifolium	B	O	•	•			•	•
Calliergon giganteum	B	O	•	•	•	•	•	•
Calliergon richardsonii	B	O			•	•	•	•
Calliergon stramineum	B	O	•	•	•	•	•	•
Calliergon trifarium	A	A	•	•		•	•	•
Calliergonella cuspidata	B	O	•	•				
Campylium calcareum	T	D	•					
Campylium cardotii	U	U		•				
Campylium chrysophyllum	B	O	•	•	•	•	•	•
Campylium halleri	B	D	•	•	•	•	•	•
Campylium hispidulum	B	E	•	•	•	•	•	•
Campylium polygamum	B	O		•	•	•	•	•
Campylium radicale	T	D	•		•		•	
Campylium stellatum	B	O	•	•	•	•	•	•
Catoscopium nigritum	B	O	•	•	•	•	•	•
Ceratodon purpureus	C		•	•	•	•	•	•
Cinclidium arcticum	A	O					•	
Cinclidium stygium	B	O	•			•	•	•
Cirryphyllum cirrosum	A	A			•		•	
*Claopodium bolanderi**	B	E	•	•	•			
Claopodium crispifolium	T	D	•					
Climacium dendroides	B	O	•	•	•	•	•	•
Conardia compacta	B	O			•	•		
Conostomum tetragonum	A	A	•	•		•	•	
*Coscinodon calyptratus**	T	E		•	•	•	•	
Coscinodon cribrosus	M	O				•		
Cratoneuron filicinum	B	O	•	•	•	•	•	•
Cynodontium alpestre	A	O				•	•	•
Cynodontium glaucescens	A	A					•	
Cynodontium schistii	A	A	•			•	•	
Cynodontium strumiferum	B	D	•	•		•	•	•
Cynodontium tenellum	B	O	•			•	•	•
Cyrtomnium hymenophylloides	A	A	•			•	•	
Desmatodon convolutus	T	D					•	
Desmatodon heimii	B	D				•	•	
Desmatodon latifolius	A	A	•	•	•	•	•	•

Species	Phytogeographic Affinity	World Distribtuion	West Slopes	Glacier National Park	Waterton Lakes National Park	Banff National Park	Jasper National Park	Willmore Wilderness Area
Desmatodon leucostoma	A	O				•		
Desmatodon obtusifolius	T	O			•	•	•	•
Desmatodon systylius	M	O			•	•	•	
Dichelyma falcatum	B	O				•	•	•
Dichelyma uncinatum	T	E		•	•			•
*Dichodontium olympicum**	M	E		•	•			
Dichodontium pellucidum	B	D	•	•	•	•	•	•
Dicranella crispa	B	O		•				•
Dicranella grevilleana	B	O	•	•		•	•	•
Dicranella heteromalla	B	O		•				
Dicranella palustris	B	D	•	•			•	•
Dicranella schreberiana	B	D	•	•	•	•		
Dicranella subulata	B	D	•	•			•	•
Dicranella varia	B	O		•		•		•
Dicranoweisia cirrata	T	D	•					
Dicranoweisia crispula	A	A	•	•	•	•	•	•
Dicranum acutifolium	A	A	•		•	•	•	•
Dicranum angustum	A	A			•	•	•	
Dicranum bonjeanii	B	O		•	•	•	•	
Dicranum brevifolium	M	O	•		•	•	•	•
Dicranum elongatum	A	A		•		•	•	•
Dicranum flagellare	B	O	•		•	•	•	•
Dicranum fragilifolium	B	O	•	•		•	•	•
Dicranum fuscescens	B	O	•	•	•	•	•	•
Dicranum groenlandicum	A	A				•	•	•
Dicranum howellii	U	U		•				
Dicranum montanum	B	D	•					
Dicranum muehlenbeckii	B	O	•	•	•	•	•	•
Dicranum ontariense	T	E					•	
*Dicranum pallidisetum**	M	E	•	•	•			
Dicranum polysetum	B	O	•	•	•	•	•	•
Dicranum scoparium	B	O	•	•	•	•	•	•
Dicranum spadiceum	A	A	•		•	•	•	
*Dicranum sulcatum**	M	E			•			
Dicranum tauricum	T	D	•	•	•			
Dicranum undulatum	B	O	•	•	•	•	•	•
Didymodon asperifolius	A	O					•	
Didymodon fallax	B	O	•		•		•	•
Didymodon johansenii	A	A				•	•	•
Didymodon nigrescens	B	D				•	•	
Didymodon rigidulus	B	O	•	•	•	•	•	•
*Didymodon subandreaeoides**	B	E				•	•	•
Didymodon tophaceus	T	O					•	

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Didymodon vinealis	T	O	•	•	•		•	•
Distichium capillaceum	C		•	•	•	•	•	•
Distichium inclinatum	B	D	•	•	•	•	•	•
Ditrichum flexicaule	B	O	•	•	•	•	•	•
Ditrichum heteromallum	T	D	•					
*Ditrichum montanum**	B	E		•	•	•		
Ditrichum pusillum	B	O	•					
Drepanocladus aduncus	C			•	•	•	•	•
Drepanocladus brevifolius	B	O			•	•		
Drepanocladus capillifolius	B	D				•		
*Drepanocladus crassicostatus**	B	E						•
Drepanocladus sendtneri	B	O	•		•		•	•
Warnstorfia tundrae	B	O				•	•	
Dryptodon patens	B	D	•	•	•			
Encalypta affinis	M	D	•	•	•	•	•	•
Encalypta alpina	A	A	•			•	•	•
Encalypta brevicolla	A	A			•	•	•	
Encalypta brevipes	A	A				•		
Encalypta ciliata	B	O	•		•	•	•	•
Encalypta intermedia	M	D			•	•		
Encalypta longicolla	M	D					•	
Encalypta mutica	M	D				•	•	
Encalypta procera	B	D	•	•	•	•	•	•
Encalypta rhaptocarpa	B	O	•	•	•	•	•	•
Encalypta spathulata	M	D			•		•	•
Encalypta vulgaris	T	D		•	•	•	•	•
Entodon concinnus	B	D					•	
Eurhynchium pulchellum	B	O	•	•	•	•	•	•
Eurynchium praelongum	T	O		•				
Fissidens adianthoides	B	D	•	•		•	•	
Fissidens bryoides	T	O	•	•	•	•	•	•
Fissidens grandifrons	T	O		•		•	•	
*Fissidens limbatus**	T	E				•		
Fissidens osmundoides	B	O		•		•	•	
Fontinalis antipyretica	B	O		•	•			
Fontinalis hypnoides	T	O		•			•	
*Fontinalis neomexicana**	T	E		•				
Funaria hygrometrica	C		•	•	•	•	•	•
Funaria muhlenbergii	T	D					•	
Grimmia affinis	B	O			•	•	•	•
Grimmia tenerrima	M	O		•	•	•	•	
Grimmia anodon	B	D	•	•	•	•	•	•
Grimmia anomala	B	D		•	•			

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*Grimmia brittoniae**	B	E		•				
Grimmia donniana	M	O			•	•	•	
Grimmia dupretii	U	E		•	•			
Grimmia elatior	T	D		•	•	•		
Grimmia incurva	M	O					•	
Grimmia mollis	M	D		•			•	
Grimmia montana	M	D		•	•	•		
Grimmia ovalis	B	O		•	•			
Grimmia plagiopodia	B	D			•			•
Grimmia pulvinata	T	O			•		•	
Grimmia teretinervis	T	D					•	
Grimmia torquata	B	D	•	•	•	•	•	•
Grimmia trichophylla	C				•		•	
Gymnostomum aeruginosum	B	O	•	•	•	•	•	
Hamatocaulis vernicosus	B	O	•	•	•	•	•	•
Hedwigia ciliata	C		•	•	•	•	•	•
Helodium blandowii	B	O	•		•		•	•
Herzogiella seligeri	T	D		•			•	
Herzogiella turfacea	B	O		•		•		
Heterocladium dimorphum	B	D	•	•	•	•	•	
*Heterocladium procurrens**	B	E	•	•	•			
*Homalothecium aeneum**	T	E	•	•	•	•	•	•
*Homalothecium nevadense**	T	E		•	•			
*Homalothecium pinnatifidum**	T	E		•	•	•	•	•
Hygrohypnum bestii	B	E	•	•	•	•	•	
Hygrohypnum cochlearifolium	M	D		•			•	
Hygrohypnum luridum	B	O	•	•	•	•	•	•
Hygrohypnum molle	B	D		•	•		•	
Hygrohypnum ochraceum	B	D	•	•	•		•	
Hygrohypnum smithii	M	O		•			•	
Hygrohypnum styriacum	M	D					•	
Hylocomiastrum umbratum	B	D	•					
Hylocomium pyrenaicum	B	O	•				•	
Hylocomium splendens	B	O	•	•	•	•	•	•
Hymenostelium recurvirostre	B	O		•	•	•	•	•
Hypnum bambergeri	A	A	•			•	•	•
Hypnum callichroum	B	O		•			•	
*Hypnum circinale**	T	E	•	•				
Hypnum cupressiforme	C		•	•	•	•	•	
Hypnum lindbergii	B	O	•		•	•	•	•
Hypnum pallescens	B	D	•		•		•	
Hypnum pratense	B	O		•	•	•	•	•
Hypnum procerrimum	A	A			•	•	•	•

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Hypnum recurvatum	B	O	•		•	•	•	•
Hypnum revolutum	B	O	•	•	•	•	•	•
Hypnum subimponens	T	D		•	•			
Hypnum vaucheri	A	A	•	•	•	•	•	•
Isopterygiopsis pulchella	B	O	•	•	•	•	•	•
*Isothecium cristatum**	T	E	•					
Isothecium myosuroides	T	D		•				
Jaffueliobryum raui	T	E					•	
Jaffueliobryum wrightii	T	E					•	
Kiaeria blyttii	M	O	•	•	•	•	•	
Kiaeria falcata	M	O	•				•	
Kiaeria glacialis	A	A					•	
Kiaeria starkei	M	O	•	•	•		•	
Leptobryum pyriforme	C		•	•	•	•	•	•
Leptodictyum humile	T	O			•	•		
Leptodictyum riparium	B	O		•	•	•		
Lescuraea saxicola	M	O			•			
Leskea obscura	T	D	•					
Leskeella nervosa	B	O	•	•	•	•	•	•
Limprichtia cossonii	U	U					•	
Limprichtia revolvens	B	O	•	•	•	•	•	•
Loeskypnum badium	A	O					•	
Meesia longiseta	B	O		•			•	
Meesia triquetra	B	O			•	•		•
Meesia uliginosa	B	O	•	•		•	•	•
Metaneckera menziesii	T	D	•	•	•	•	•	•
Mielichhoferia macrocarpa	M	E					•	
Mielichhoferia mielichhofer	M	O	•					
Mnium ambiguum	B	O	•	•	•	•	•	•
Mnium arizonicum	M	D	•		•	•	•	•
Mnium blyttii	A	A	•	•	•	•	•	•
Mnium marginatum	B	O	•	•	•	•		•
Mnium spinosum	B	D	•			•		
Mnium spinulosum	B	D	•	•	•	•	•	•
Mnium thomsonii	B	O	•		•	•	•	•
Molendoa sendtneriana	A	A				•	•	
Myurella julacea	B	O	•	•	•	•	•	•
Myurella sibirica	T	O					•	
Myurella tenerrima	A	A		•		•	•	•
Neckera pennata	B	D	•				•	•
Oligotrichum aligerum	T	D	•					
Oligotrichum hercynicum	M	O	•	•			•	
Oligotrichum parallelum	B	D	•				•	

Species	Phytogeographic Affinity	World Distribtuion	West Slopes	Glacier National Park	Waterton Lakes National Park	Banff National Park	Jasper National Park	Willmore Wilderness Area
Oncophorus virens	B	O	•	•	•	•	•	•
Oncophorus wahlenbergii	B	O	•	•	•	•	•	•
Oreas martiana	A	O						•
Orthothecium chryseum	A	A	•	•	•	•	•	•
Orthothecium intricatum	M	O	•			•	•	•
Orthothecium strictum	A	A				•	•	•
Orthotrichum affine	T	D		•	•	•	•	
Orthotrichum alpestre	B	D	•	•	•	•	•	•
Orthotrichum anomalum	B	O	•		•	•	•	•
Orthotrichum cupulatum	T	O	•	•				
Orthotrichum laevigatum	T	D	•	•	•	•	•	•
Orthotrichum lyellii	T	D		•				
Orthotrichum obtusifolium	B	O	•	•	•	•	•	•
Orthotrichum pallens	B	D	•		•	•	•	•
Orthotrichum pellucidum	T	D	•		•	•	•	•
Orthotrichum pulchellum	T	D			•			
Orthotrichum pumilum	T	D		•	•			
Orthotrichum pylaisii	A	A				•	•	•
Orthotrichum rupestre	T	O	•	•	•	•	•	•
Orthotrichum speciosum	B	O	•	•	•	•	•	•
Orthotrichum striatum	T	D		•				
Paludella squarrosa	B	O	•	•		•	•	•
Palustriella commutata	B	O	•	•	•	•	•	•
Paraleucobryum enerve	T	D	•	•	•	•	•	•
Paraleucobryum longifolium	B	O	•	•				
Philonotis fontana	B	O	•	•	•	•	•	•
Philonotis marchica	B	O					•	•
Philonotis yezoana	B	D			•			
*Physcomitrium pyriforme**	T	E	•					
Plagiobryum demissum	M	O				•	•	
Plagiobryum zieri	M	O	•	•	•	•	•	•
Plagiomnium ciliare	B	E		•	•	•		
Plagiomnium cuspidatum	B	O		•	•	•	•	•
Plagiomnium drummondii	B	O	•	•	•	•	•	
Plagiomnium ellipticum	B	O	•	•	•	•	•	•
*Plagiomnium insigne**	T	E	•	•	•			
Plagiomnium medium	B	O	•	•	•	•	•	•
Plagiomnium rostratum	C			•	•	•		
*Plagiomnium venustum**	T	E		•				
Plagiopus oederiana	B	O	•	•	•	•		•
Plagiothecium cavifolium	T	D	•	•	•			
Plagiothecium denticulatum	B	O	•	•	•	•	•	•
Plagiothecium laetum	B	D	•	•	•		•	•

Species	Phytogeographic Affinity	World Distribution	West Slopes	Glacier National Park	Waterton Lakes National Park	Banff National Park	Jasper National Park	Willmore Wilderness Area
Plagiothecium piliferum	T	D	•	•				
Platydictya jungermannioides	B	O	•	•	•	•	•	•
Platydictya minutissima	T	E					•	
Pleurozium schreberi	B	O	•	•	•	•	•	•
Pogonatum dentatum	B	O	•				•	•
Pogonatum urnigerum	B	O	•	•	•	•	•	•
Pohlia annotina	T	O	•	•	•		•	
Pohlia atropurpurea	A	A	•		•			
Pohlia bolanderi	A	A			•			
Pohlia brevinervis	A	A					•	
*Pohlia cardotii**	M	E	•					
Pohlia cruda	B	O	•	•	•	•	•	•
Pohlia crudoides	A	A					•	
Pohlia drummondii	M	O	•	•	•	•	•	
Pohlia elongata	B	D	•			•	•	
Pohlia filum	B	D					•	
*Pohlia longibracteata**	T	E	•					
Pohlia longicolla	B	O	•					
Pohlia nutans	B	O	•	•	•	•	•	•
Pohlia obtusifolia	M	O	•	•	•		•	
Pohlia proligera	B	O	•		•	•	•	•
Pohlia sphagnicola	B	O			•	•	•	•
Pohlia vexans	B	D	•				•	•
Pohlia wahlenbergii	C		•	•	•	•	•	•
Polytrichastrum alpinum	B	O	•	•	•	•	•	•
Polytrichum commune	C		•	•	•	•	•	•
Polytrichum formosum	B	O	•	•				
Polytrichum juniperinum	C		•	•	•	•	•	•
Polytrichum longisetum	B	O	•				•	
*Polytrichum lyallii**	M	E	•	•	•	•	•	
Polytrichum piliferum	C		•	•	•	•	•	•
Polytrichum sexangulare	M	O	•				•	
Polytrichum strictum	B	O	•	•	•	•	•	•
Pseudocalliergon turgescens	A	A	•	•	•	•	•	•
*Pseudoleskea atricha**	T	E			•		•	
Pseudoleskea incurvata	B	O	•	•	•	•	•	•
Pseudoleskea patens	M	D		•	•	•		
Pseudoleskea radicosa	M	O	•	•	•	•	•	•
Pseudoleskea stenophylla	T	E	•	•	•		•	
Pseudoleskeella sibirica	U	D			•	•	•	•
Pseudoleskeella tectorum	B	D	•	•	•	•	•	•
Pseudotaxiphyllum elegans	T	O	•					
Pterigynandrum filiforme	B	O	•	•	•	•	•	•

Species	Phytogeographic Affinity	World Distribtuion	West Slopes	Glacier National Park	Waterton Lakes National Park	Banff National Park	Jasper National Park	Willmore Wilderness Area
Pterygoneurum ovatum	T	O					•	
Pterygoneurum subsessile	T	O	•				•	
Ptilium crista-castrensis	B	O	•	•	•	•	•	•
Pylaisiella polyantha	B	O	•	•	•	•	•	•
Racomitrium aciculare	B	O	•	•		•	•	
Racomitrium canescens	B	O	•	•	•	•	•	•
Racomitrium elongatum	T	O	•		•			
Racomitrium ericoides	T	O	•					
Racomitrium fasciculare	B	O	•	•			•	
Racomitrium heterostichum	B	D	•	•	•	•	•	
Racomitrium lanuginosum	C		•	•	•	•	•	
*Racomitrium lawtonae**	B	E	•					
Racomitrium microcarpon	U	U			•		•	
Racomitrium sudeticum	B	O	•	•	•	•	•	
Rhizomnium andrewsianum	A	A					•	•
*Rhizomnium glabrescens**	T	E	•	•				
Rhizomnium gracile	B	D			•	•	•	•
Rhizomnium magnifolium	B	O	•	•	•	•	•	•
Rhizomnium nudum	M	D	•	•	•		•	
Rhizomnium pseudopunctatum	B	O	•	•	•	•	•	•
Rhizomnium punctatum	B	D	•	•		•	•	
Rhytidiadelphus loreus	B	D		•				
Rhytidiadelphus squarrosus	B	D	•	•	•		•	
Rhytidiadelphus triquetrus	B	O	•	•	•	•	•	•
*Rhytidiopsis robusta**	M	E	•	•	•	•	•	
Rhytidium rugosum	A	A	•	•	•	•	•	•
*Roellia roellii**	M	E	•	•	•	•	•	
Saelania glaucescens	B	O				•	•	•
Sanionia uncinata	C		•	•	•	•	•	•
Sarmenthypnum sarmentosum	A	A	•	•		•	•	
Schistidium agassizii	B	D		•	•		•	
Schistidium apocarpum	C		•	•	•	•	•	•
Schistidium rivulare	B	D	•	•	•	•	•	•
Schistidium tenerum	A	A			•	•	•	
Schistidium trichodon	B	D	•				•	
Schistostega pennata	T	O		•				
*Scleropodium obtusifolium**	T	E		•				
Scleropodium touretii	T	D		•				
Scorpidium scorpioides	B	O	•		•	•	•	•
Scouleria aquatica	T	D	•	•	•	•	•	•
Seligeria calcarea	B	D			•	•		
Seligeria campylopoda	B	D	•	•	•	•	•	•
Seligeria donniana	B	D			•		•	•

Species	Phytogeographic Affinity	World Distribtuion	West Slopes	Glacier National Park	Waterton Lakes National Park	Banff National Park	Jasper National Park	Willmore Wilderness Area
Seligeria subimmersa	M	D					•	•
Seligeria tristichoides	B	D					•	
Sphagnum angustifolium	B	O	•		•		•	•
Sphagnum capillifolium	B	D		•	•	•	•	•
Sphagnum centrale	B	O	•					
Sphagnum compactum	B	O	•				•	
Sphagnum fallax	B	O	•					
Sphagnum fimbriatum	B	O	•				•	
Sphagnum fuscum	B	O	•	•		•	•	•
Sphagnum girgensohnii	B	O	•	•	•		•	•
Sphagnum jensenii	B	D						•
Sphagnum lindbergii	B	O	•				•	
Sphagnum magellanicum	C		•					•
Sphagnum majus	B	O						•
Sphagnum platyphyllum	B	O					•	
Sphagnum riparium	B	D	•		•			
Sphagnum russowii	B	D	•	•	•	•	•	•
Sphagnum squarrosum	B	O	•	•	•		•	
Sphagnum subsecundum	C		•	•				
Sphagnum teres	B	O	•	•	•	•	•	
Sphagnum warnstorfii	B	O	•	•	•	•	•	•
Sphagnum wulfianum	B	D	•					•
Splachnum sphaericum	B	D				•	•	•
Splachnum vasculosum	A	A				•		
Stegonia latifolia	A	A	•	•		•	•	
Stegonia pilifera	U	U				•	•	
Tayloria froehlichiana	A	A				•	•	
Tayloria hornschuchii	A	A				•		
Tayloria ligulata	B	O	•	•		•	•	•
Tayloria serrata	B	D	•	•	•		•	•
Tetraphis geniculata	B	D	•					
Tetraphis pellucida	B	O	•	•	•	•	•	•
Tetraplodon angustatus	B	O	•		•	•	•	•
Tetraplodon mnioides	B	O	•			•	•	•
Tetraplodon urceolatus	A	A					•	•
*Thamnobryum neckeroides**	T	E		•	•			
Thuidium recognitum	B	O	•	•	•	•	•	•
Timmia austriaca	A	A	•	•	•	•	•	•
Timmia megapolitana	T	O	•	•	•	•	•	•
Timmia norvegica	A	A		•		•		•
Timmia sibirica	A	A				•		
Tomenthypnum falcifolium	B	E	•					•
Tomenthypnum nitens	B	O	•	•	•	•	•	•

Species	Phytogeographic Affinity	World Distribtuion	West Slopes	Glacier National Park	Waterton Lakes National Park	Banff National Park	Jasper National Park	Willmore Wilderness Area
Tortella fragilis	B	O	•	•	•	•	•	•
Tortella humilis	T	D		•				
Tortella inclinata	T	D	•	•	•	•	•	
Tortella tortuosa	B	O	•	•	•	•	•	•
Tortula bartramii	U	E			•			
Tortula caninervis	T	D			•			
Tortula mucronifolia	B	O		•	•	•	•	•
Tortula muralis	C		•					
Tortula norvegica	A	A	•	•	•	•	•	•
*Tortula papillosissima**	M	E			•			
Tortula ruralis	B	O	•	•	•	•	•	•
Tortula subulata	B	O		•	•			
Trichodon cylindricus	B	D	•	•		•		
Ulota crispa	B	O					•	
Ulota curvifolia	B	O	•				•	
Voitia nivalis	A	A				•	•	
*Warnstorfia exannulata**	B	O	•	•	•	•	•	•
Warnstorfia fluitans	B	O	•	•	•		•	
Warnstorfia pseudostraminea	B	O			•			
Warnstorfia trichophylla	B	D	•					
Weissia controversa	C			•	•			
Total Flora			285	280	288	271	344	226

Appendix B. Species data for 112 sites (corresponding to columns 1 to 112) sampled in Waterton Lakes National Park in Summer, 1997. "Freq" refers to the frequency (number of sites) of each species' occurrence. Names are standardized to the North American checklists (Anderson 1990; Anderson et al. 1990) with the following exceptions: Amblystegium juratzkanum Schimp., Brachythecium asperrimum (Mitt. ex Müll. Hal.) Sull., Bryum elegans Nees, Dicranum sulcatum Müll. Hal., Grimmia atricha Müll. Hal. & Kindb., and Grimmia dupretii Thér.. These species were considered distinct for the purposes of the current study.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
[illegible]																1				
Amblystegium juratzkanum									1									1		
[illegible]			1	1		1	1	1	1	1	1							1		1
Amblystegium varium																				
[illegible]																1				
Andreaea rupestris																				
[illegible]											1									
Atrichum selwynii			1																	
[illegible]																	1			
Aulacomnium palustre									1									1	1	1
[illegible]																				
Barbula convoluta																				
[illegible]																				
Barbula unguiculata																				
[illegible]																				
Blindia acuta																				
[illegible]	1	1	1	1	1								1		1		1			1
Brachythecium asperrimum																				
[illegible]					1									1						
Brachythecium campestre																				
[illegible]			1		1						1	1	1	1			1	1		1
Brachythecium erythrorrhizon	1		1	1													1			1
[illegible]																				
Brachythecium frigidum																1		1		
[illegible]			1		1															
Brachythecium leibergii			1		1								1	1	1		1			
[illegible]									1									1	1	
Brachythecium nelsonii									1											1
[illegible]			1		1												1			1
Brachythecium plumosum																				
[illegible]			1																	
Brachythecium rivulare									1											
[illegible]																				
Brachythecium salebrosum	1		1	1		1	1	1	1	1			1							1
[illegible]																			1	
Brachythecium velutinum		1		1		1	1						1	1		1	1			
[illegible]	1		1										1	1	1	1				
Bryum algovicum																				
[illegible]		1																		
Bryum caespiticium												1		1						
[illegible]																				
Bryum capillare			1		1						1		1			1	1			
[illegible]																				
Bryum elegans		1																		
[illegible]									1	1	1				1		1	1	1	
Bryum miniatum											1									
[illegible]																				
Bryum pallescens																				
[illegible]									1		1							1		
Bryum stirtonii		1																		
[illegible]																				
Calliergon giganteum																				
[illegible]																				
Campylium chrysophyllum															1					1
[illegible]																				
Campylium hispidulum									1									1		
[illegible]									1											
Campylium radicale																				
[illegible]																		1	1	
Catascopium nigritum																				
[illegible]				1							1	1		1			1	1		1
Cinclidium cirrosum																				
[illegible]																				
Climacium dendroides									1									1		
[illegible]																				
Coscinodon calyptratus																				
[illegible]											1							1		
Desmatodon latifolius	1										1									
[illegible]																				
Dichodontium olympicum																				
[illegible]																				
Dicranella schreberiana																				
[illegible]		1													1					
Dicranum acutifolium																				
[illegible]		1																		
Dicranum brevifolium			1																	
[illegible]																				
Dicranum fuscescens																				
[illegible]																				
Dicranum pallidisetum																				

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
[illegible]																			1	
Dicranum scoparium	1		1		1								1	1	1	1			1	1
[illegible]																				
Dicranum undulatum																			1	
[illegible]																				
Didymodon rigidulus											1									
[illegible]	1										1				1					
Distichium capillaceum	1														1	1			1	
[illegible]																				
Ditrichum flexicaule	1				1						1				1	1				
[illegible]									1									1		
Drepanocladus brevifolius																				
[illegible]																				
Dryptodon patens																				
[illegible]	1																			
Encalypta ciliata												1								
[illegible]																				
Encalypta procera														1	1	1				
[illegible]	1										1					1				
Encalypta spathulata																				
[illegible]												1								
Eurhynchium pulchellum	1	1	1		1								1		1	1		1		1
[illegible]														1						
Fontinalis antipyretica																				
[illegible]																				
Grimmia affinis																				
[illegible]											1						1			
Grimmia anomala																				
[illegible]																				
Grimmia dupretii	1		1		1		1				1		1	1	1	1				
[illegible]													1							
Grimmia montana												1				1				
[illegible]																				
Grimmia tenerrima	1										1					1				
[illegible]																				
Grimmia trichophylla																				
[illegible]											1				1					
Hamatocaulis vernicosus																				
[illegible]																				
Helodium blandowii									1									1		1
[illegible]																				
Heterocladium procurrens																				
[illegible]	1				1						1		1	1	1	1	1			
Homalothecium nevadense																1				
[illegible]	1										1									
Hygrohypnum bestii																				
[illegible]																				
Hygrohypnum molle																				
[illegible]																				
Hylocomium splendens													1						1	1
[illegible]																				
Hypnum cupressiforme														1		1	1			
[illegible]																		1		
Hypnum pallescens					1															
[illegible]																			1	
Hypnum recurvatum																				
[illegible]	1		1	1	1	1		1		1	1		1	1	1	1	1			1
Hypnum vaucheri											1					1	1			
[illegible]			1																	
Kiaeria starkei																				
[illegible]									1									1		1
Leptodictyum humile									1											
[illegible]																			1	
Lescuraea saxicola		1																		
[illegible]			1										1	1	1		1			
Limprichtia revolvens																		1		
[illegible]																				
Mnium ambiguum				1									1							
[illegible]		1	1		1								1	1						1
Mnium blyttii																				
[illegible]	1								1											
Mnium spinulosum			1	1	1	1							1	1			1			1
[illegible]	1		1													1				
Myurella julacea																1				
[illegible]			1										1	1			1			1
Orthothecium chryseum																				
[illegible]							1													
Orthotrichum alpestre						1				1				1	1	1	1			
[illegible]																	1			
Orthotrichum laevigatum					1						1	1	1	1	1	1	1			

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
[illegible]											1									
Orthotrichum pallens														1		1	1			
[illegible]											1					1	1			
Orthotrichum pulchellum																				
[illegible]											1									
Orthotrichum speciosum						1	1						1							
[illegible]																				
Paraleucobryum enerve																				
[illegible]									1		1							1		
Philonotis yezoana																				
[illegible]																				
Plagiomnium cuspidatum							1													
[illegible]	1								1									1		
Plagiomnium insigne																				
[illegible]	1																			
Plagiopus oederiana																				
[illegible]																				
Plagiothecium denticulatum		1	1																	
[illegible]			1		1									1						
Platydictya jungermannioides	1		1								1		1	1	1	1	1	1	1	
[illegible]			1		1								1						1	1
Pogonatum urnigerum		1																		
[illegible]																				
Pohlia bolanderi																				
[illegible]	1											1			1					
Pohlia drummondii																				
[illegible]			1		1											1	1	1	1	1
Pohlia obtusifolia																				
[illegible]																				
Pohlia sphagnicola																			1	1
[illegible]																				
Polytrichastrum alpinum		1																		
[illegible]																				
Polytrichum juniperinum			1								1	1	1			1	1			
[illegible]																				
Polytrichum piliferum		1																		
[illegible]																		1		
Pseudocalliergon turgescens																				
[illegible]																				
Pseudoleskea incurvata	1		1								1			1	1	1	1			
[illegible]	1																			
Pseudoleskea radicosa	1	1	1		1		1			1			1	1	1		1			
[illegible]																				
Pseudoleskeella sibirica																1				
[illegible]					1						1	1	1	1	1	1	1			
Pterigynandrum filiforme														1			1			
[illegible]					1															1
Pylaisiella polyantha				1		1	1	1		1							1	1		
[illegible]	1																			
Racomitrium heterostichum																1				
[illegible]																				
Racomitrium sudeticum																				
[illegible]																				
Rhizomnium magnifolium																				
[illegible]																				
Rhizomnium pseudopunctatum																				1
[illegible]																				
Rhytidiadelphus triquetrus	1													1						1
[illegible]			1		1								1	1						1
Rhytidium rugosum		1																		
[illegible]														1						
Sanionia uncinata	1	1	1		1										1			1	1	1
[illegible]																				
Schistidium apocarpum											1		1	1	1	1				
[illegible]	1										1					1				
Schistidium tenerum					1															
[illegible]																		1		
Scouleria aquatica																				
[illegible]																				
Seligeria campylopoda																				
[illegible]																				
Sphagnum angustifolium																				
[illegible]																				
Sphagnum russowii																			1	1
[illegible]																				
Sphagnum teres																				
[illegible]																		1	1	1
Tayloria serrata																				
[illegible]																				
Tetraplodon angustatus																				1

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
[illegible]																				
Timmia austriaca	1		1		1									1		1				
[illegible]	1																			
Tomenthypnum nitens									1									1	1	1
[illegible]											1									
Tortella inclinata																				
[illegible]	1		1		1						1		1	1	1	1				
Tortula bartramii											1									
[illegible]																				
Tortula mucronifolia					1								1	1		1	1			
[illegible]	1	1	1		1								1		1	1				
Tortula papillosissima																				
[illegible]	1			1	1						1	1	1	1	1	1	1			1
Tortula subulata																				
[illegible]																				
Warnstorfia pseudostraminea																				
[illegible]																				

Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
[illegible]													1				1			
Amblystegium juratzkanum		1				1	1	1										1		
[illegible]		1		1	1	1	1	1								1	1	1		
Amblystegium varium				1																
[illegible]																				
Andreaea rupestris																				
[illegible]																				
Atrichum selwynii												1								
[illegible]				1	1							1								
Aulacomnium palustre		1		1		1	1													
[illegible]																				
Barbula convoluta												1								
[illegible]																				
Barbula unguiculata										1										
[illegible]																				
Blindia acuta																				
[illegible]		1			1	1			1	1		1		1				1	1	
Brachythecium asperrimum																				
[illegible]				1					1			1							1	
Brachythecium campestre																				
[illegible]									1			1								
Brachythecium erythrorrhizon				1						1			1					1		
[illegible]					1															
Brachythecium frigidum		1					1						1							
[illegible]												1						1	1	
Brachythecium leibergii		1			1				1			1	1					1	1	
[illegible]		1				1	1	1												
Brachythecium nelsonii		1											1							
[illegible]						1						1						1	1	
Brachythecium plumosum																				
[illegible]					1													1	1	
Brachythecium rivulare													1				1			
[illegible]								1												
Brachythecium salebrosum					1	1	1		1			1	1					1	1	
[illegible]	1			1		1		1												
Brachythecium velutinum					1							1		1				1		
[illegible]				1	1	1		1		1		1	1				1			1
Bryum algovicum																				
[illegible]										1				1						
Bryum caespiticium								1						1	1					
[illegible]																				
Bryum capillare		1			1	1						1	1							
[illegible]																				
Bryum elegans																				
[illegible]				1	1	1								1		1				
Bryum miniatum																				
[illegible]																				
Bryum pallescens	1			1		1														
[illegible]	1	1		1		1	1	1								1		1		
Bryum stirtonii																				
[illegible]																				
Calliergon giganteum																				
[illegible]																				
Campylium chrysophyllum				1		1												1		
[illegible]													1							
Campylium hispidulum				1														1		
[illegible]																		1		
Campylium radicale																				
[illegible]	1	1		1			1						1							
Catascopium nigritum		1																		
[illegible]						1			1	1				1			1			
Cirriphyllum cirrosum																				
[illegible]													1							
Climacium dendroides																				
[illegible]						1		1								1				
Coscinodon calyptratus																				
[illegible]		1		1												1	1			
Desmatodon latifolius																				
[illegible]																				
Dichodontium olympicum																				
[illegible]																				
Dicranella schreberiana																				
[illegible]												1								
Dicranum acutifolium																				
[illegible]																				
Dicranum brevifolium																		1		
[illegible]																				
Dicranum fuscescens												1							1	
[illegible]																				
Dicranum pallidisetum																				

Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
[illegible]				1																
Dicranum scoparium		1		1	1							1						1	1	
[illegible]																			1	
Dicranum undulatum																				
[illegible]																				
Didymodon rigidulus													1							
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Distichium capillaceum	1			1	1					1										1
[illegible]																				
Ditrichum flexicaule				1						1	1		1			1	1	1	1	1
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Drepanocladus brevifolius			1																	
[illegible]																				
Dryptodon patens																			1	
[illegible]																				
Encalypta ciliata				1										1						
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Encalypta procera																				1
[illegible]					1									1						
Encalypta spathulata														1						
[illegible]										1				1			1			
Eurhynchium pulchellum				1	1	1				1		1	1				1			
[illegible]												1								
Fontinalis antipyretica																				
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Grimmia affinis																				
[illegible]									1		1			1						
Grimmia anomala																				
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Grimmia dupretii				1	1				1		1	1	1			1			1	1
[illegible]																				
Grimmia montana																				
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Grimmia tenerrima																				
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Grimmia trichophylla																				
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Hamatocaulis vernicosus	1												1							
[illegible]																				
Helodium blandowii																				
[illegible]																				
Heterocladium procurrens																				
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Homalothecium nevadense																				1
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Hygrohypnum bestii																				
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Hygrohypnum molle																				
[illegible]																				
Hylocomium splendens				1								1							1	
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Hypnum cupressiforme																				
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Hypnum pallescens																	1			
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Hypnum recurvatum																				
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Hypnum vaucheri					1					1	1									
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Kiaeria starkei																				
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Leptodictyum humile		1																		
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Lescuraea saxicola					1															
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Limprichtia revolvens	1			1														1		
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Mnium blyttii										1										
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Mnium spinulosum				1	1							1						1		
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Myurella julacea																1				
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Orthothecium chryseum													1							
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Orthotrichum alpestre					1															1
[illegible]						1														
Orthotrichum laevigatum				1	1															1

Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
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[illegible]																				1
Orthotrichum pulchellum																				
[illegible]						1														
Orthotrichum speciosum				1		1														
[illegible]	1			1												1				
Paraleucobryum enerve																				
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Philonotis yezoana																				
[illegible]																				
Plagiomnium cuspidatum						1														
[illegible]		1				1	1										1			
Plagiomnium insigne																				
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Plagiopus oederiana				1																
[illegible]																				
Plagiothecium denticulatum																				
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Platydictya jungermannioides		1		1	1	1				1		1	1							1
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Pogonatum urnigerum																				
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Pohlia bolanderi																				
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Pohlia drummondii																				
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Pohlia obtusifolia																				
[illegible]																				
Pohlia sphagnicola																				
[illegible]						1				1						1	1	1		
Polytrichastrum alpinum												1								
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Polytrichum juniperinum				1																
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Polytrichum piliferum																				
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Pseudocalliergon turgescens																				
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Pseudoleskea radicosa					1							1	1				1	1	1	
[illegible]					1								1					1		
Pseudoleskeella sibirica																				
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Pterigynandrum filiforme					1							1								
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Pylaisiella polyantha		1				1		1	1											
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Racomitrium heterostichum																				
[illegible]																				
Racomitrium sudeticum																				
[illegible]																				
Rhizomnium magnifolium																				
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Rhizomnium pseudopunctatum																				
[illegible]																				
Rhytidiadelphus triquetrus												1								
[illegible]												1						1	1	
Rhytidium rugosum																				
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Sanionia uncinata				1	1	1						1	1					1	1	
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[illegible]													1			1			1	
Schistidium tenerum																				
[illegible]	1																			
Scouleria aquatica																				
[illegible]																				
Seligeria campylopoda																				
[illegible]																				
Sphagnum angustifolium																				
[illegible]																				
Sphagnum russowii																				
[illegible]																				
Sphagnum teres																				
[illegible]																				
Taylonia serrata																				
[illegible]												1								
Tetraplodon angustatus																				

Species	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
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[illegible]												1								
Tomenthypnum nitens							1													
[illegible]						1											1			
Tortella inclinata											1		1							
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Tortula bartramii														1						
[illegible]											1									
Tortula mucronifolia				1	1					1				1	1		1			
[illegible]				1	1															
Tortula papillosissima																				
[illegible]		1		1	1	1			1	1	1			1	1		1		1	1
Tortula subulata												1								
[illegible]																				
Warnstorfia pseudostramines													1							
[illegible]																	1			

Species	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
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Amblystegium varium																				
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Andreaea rupestris																				
[illegible]																				
Atrichum selwynii			1						1									1		
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Aulacomnium palustre				1		1	1					1					1			1
[illegible]																				
Barbula convoluta																				
[illegible]			1																	
Barbula unguiculata										1										
[illegible]																	1	1		
Blindia acuta																				
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Brachythecium asperrimum												1						1		
[illegible]					1															
Brachythecium campestre														1						
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Brachythecium erythrorrhizon	1		1			1	1		1			1			1		1	1		
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Brachythecium frigidum																		1		
[illegible]			1				1	1	1						1					
Brachythecium leibergii			1				1		1						1					
[illegible]																			1	1
Brachythecium nelsonii						1	1					1						1		
[illegible]			1					1							1			1		
Brachythecium plumosum																				
[illegible]			1												1		1	1		
Brachythecium rivulare							1											1		
[illegible]																				1
Brachythecium salebrosum		1	1			1	1		1	1				1	1		1	1		1
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Brachythecium velutinum			1												1		1	1		
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[illegible]	1	1		1																
Bryum caespiticium		1		1					1				1	1						
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Bryum capillare	1								1								1			
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Bryum elegans																				
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Bryum miniatum				1																
[illegible]																				
Bryum pallescens																				
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Bryum stirtonii				1												1	1			
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Calliergon giganteum							1													
[illegible]						1														
Campylium chrysophyllum	1																			
[illegible]									1											
Campylium hispidulum																				
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Campylium radicale																				1
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Catascopium nigritum																				
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Cirriphyllum cirrosum																				
[illegible]																		1		
Climacium dendroides																				
[illegible]									1											
Coscinodon calyptratus																				
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Desmatodon latifolius				1										1						
[illegible]																				
Dichodontium olympicum																				
[illegible]													1					1		
Dicranella schreberiana												1								
[illegible]		1												1		1	1	1		
Dicranum acutifolium																				
[illegible]																				
Dicranum brevifolium																				
[illegible]								1												
Dicranum fuscescens							1	1							1			1		
[illegible]							1	1												
Dicranum pallidisetum								1												

Species	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Dicranum scoparium		1	1			1		1	1						1	1	1			
Dicranum undulatum																				
Didymodon rigidulus	1								1											
Distichium capillaceum	1	1							1									1		
Ditrichum flexicaule	1	1		1					1	1										
Drepanocladus brevifolius																				
Dryptodon patens																1	1			
Encalypta ciliata				1																
Encalypta procera	1								1											
Encalypta spathulata																				
Eurhynchium pulchellum			1	1	1				1						1	1	1	1		
Fontinalis antipyretica																				
Grimmia affinis																				
Grimmia anomala																				
Grimmia dupretii	1	1		1												1				
Grimmia montana				1												1				
Grimmia tenerrima				1										1						
Grimmia trichophylla	1																			
Hamatocaulis vernicosus																		1		
Helodium blandowii																				
Heterocladium procurrens			1														1			
Homalothecium nevadense																				
Hygrohypnum bestii																		1		
Hygrohypnum molle																		1		
Hylocomium splendens		1							1							1		1		
Hypnum cupressiforme	1								1											
Hypnum pallescens							1													
Hypnum recurvatum																				
Hypnum vaucheri	1								1											
Kiaeria starkei																1	1			
Leptodictyum humile																				
Lescuraea saxicola																				
Limprichtia revolvens							1										1			
Mnium ambiguum				1														1		
Mnium blyttii							1					1						1		
Mnium spinulosum			1						1						1		1	1		
Myurella julacea									1											
Orthothecium chryseum																				
Orthotrichum alpestre																				
Orthotrichum laevigatum				1																

Species	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Orthotrichum pallens																				
Orthotrichum pulchellum																				
Orthotrichum speciosum																				1
Paraleucobryum enerve																	1			
Philonotis yezoana																				
Plagiomnium cuspidatum																			1	1
Plagiomnium insigne															1					
Plagiopus oederiana									1											
Plagiothecium denticulatum						1	1								1		1	1		
Platydictya jungermannioides			1						1									1		
Pogonatum urnigerum																				
Pohlia bolanderi					1											1	1			
Pohlia drummondii																1				
Pohlia obtusifolia																				
Pohlia sphagnicola						1	1													
Polytrichastrum alpinum																1	1	1		
Polytrichum juniperinum			1	1	1	1	1		1						1					
Polytrichum piliferum				1	1											1				
Pseudocalliergon turgescens																				
Pseudoleskea incurvata		1																		
Pseudoleskea radicosa		1	1	1									1	1	1	1	1	1		
Pseudoleskeella sibirica																				
Pterigynandrum filiforme	1																			
Pylaisiella polyantha																				1
Racomitrium heterostichum	1															1	1			
Racomitrium sudeticum																				
Rhizomnium magnifolium						1	1					1						1		
Rhizomnium pseudopunctatum						1	1													
Rhytidiadelphus triquetrus									1											
Rhytidium rugosum																				
Sanionia uncinata	1	1	1			1	1		1			1			1	1	1	1		1
Schistidium apocarpum	1			1										1		1	1			
Schistidium tenerum																				
Scouleria aquatica																				
Seligeria campylopoda									1											
Sphagnum angustifolium						1														
Sphagnum russowii						1	1													
Sphagnum teres						1	1													
Taylonia serrata																				
Tetraplodon angustatus																				

Species	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Timmia austriaca		1		1					1			1				1	1	1		
Tomenthypnum nitens																				
Tortella inclinata																				
Tortula bartramii																				
Tortula mucronifolia		1	1																	
Tortula papillosissima																				
Tortula subulata									1											
Warnstorfia pseudostraminea																				

Species	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
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Amblystegium juratzkanum					1										1					
[illegible]					1									1	1			1		
Amblystegium varium																				
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Andreaea rupestris																				
[illegible]																				
Atrichum selwynii																				
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Aulacomnium palustre	1					1					1									
[illegible]	1										1									
Barbula convoluta																				
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Barbula unguiculata																				
[illegible]																				
Blindia acuta																				
[illegible]			1			1												1		1
Brachythecium asperrimum	1					1														
[illegible]												1								
Brachythecium campestre																				
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Brachythecium erythrorrhizon	1			1		1					1				1					1
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Brachythecium frigidum	1					1														
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Brachythecium leibergii			1	1		1			1	1				1	1					
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Brachythecium nelsonii	1										1									
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Brachythecium plumosum															1					
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Brachythecium salebrosum				1		1				1				1	1			1		
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Bryum caespiticium					1		1					1	1	1		1				
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Bryum miniatum																				
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Bryum pallescens									1									1		
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Bryum stirtonii																				1
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Calliergon giganteum																				
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Campylium chrysophyllum														1	1					
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Campylium hispidulum																				
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Catascopium nigritum																				
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Cirriphyllum cirrosum																				
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Climacium dendroides																				
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Coscinodon calyptratus																			1	
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Desmatodon latifolius	1		1	1	1				1			1				1	1			
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Dichodontium olympicum																				
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Dicranella schreberiana																				
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Dicranum brevifolium											1									
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Dicranum fuscescens				1						1										
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Dicranum pallidisetum																				

Species	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
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Dicranum scoparium				1		1										1				
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Dicranum undulatum																				
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Distichium capillaceum			1		1	1														
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Ditrichum flexicaule			1		1	1								1						1
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Drepanocladus brevifolius																				
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Dryptodon patens																				
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Eurhynchium pulchellum			1			1		1				1				1		1		
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Fontinalis antipyretica											1									
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Grimmia affinis																				
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Grimmia anomala	1					1														
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Grimmia dupretii							1	1	1											1
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Grimmia montana					1		1						1				1			1
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Grimmia tenerrima								1												1
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Grimmia trichophylla																				
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Heterocladium procurrens																				
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Homalothecium nevadense					1															
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Hygrohypnum bestii	1					1														
[illegible]	1					1		1												
Hygrohypnum molle																				
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Hylocomium splendens										1										
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Hypnum cupressiforme														1						
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Hypnum pallescens														1						
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Hypnum recurvatum																				
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Hypnum vaucheri					1															1
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Kiaeria starkei																				
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Leptodictyum humile																				
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Mnium ambiguum																				
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Mnium blyttii						1														
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Mnium spinulosum				1		1				1				1						
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Myurella julacea			1		1															
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Orthothecium chryseum																				
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Orthotrichum alpestre						1												1		
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Orthotrichum laevigatum					1	1								1					1	1

Species	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
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Orthotrichum pulchellum																				
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Orthotrichum speciosum																		1		
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Paraleucobryum enerve																				
[illegible]	1				1	1		1			1									
Philonotis yezoana																				
[illegible]																				
Plagiomnium cuspidatum															1					
[illegible]																				
Plagiomnium insigne																				
[illegible]		1				1									1					
Plagiopus oederiana																				
[illegible]																				
Plagiothecium denticulatum											1									
[illegible]						1				1										
Platydictya jungermannioides					1	1		1												
[illegible]				1																
Pogonatum urnigerum	1																			
[illegible]																				
Pohlia bolanderi	1											1	1			1	1			
[illegible]			1			1		1		1						1	1	1		
Pohlia drummondii																				
[illegible]				1					1	1	1						1			
Pohlia obtusifolia					1															
[illegible]																				
Pohlia sphagnicola																				
[illegible]	1					1					1									
Polytrichastrum alpinum										1										
[illegible]																				
Polytrichum juniperinum	1	1		1		1				1	1		1							
[illegible]	1	1																		
Polytrichum piliferum		1			1	1											1			
[illegible]																				
Pseudocalliergon turgescens																				
[illegible]																		1		
Pseudoleskea incurvata			1		1			1										1		1
[illegible]	1					1														
Pseudoleskea radicosa	1	1	1	1		1		1	1	1	1			1	1			1		1
[illegible]																		1		
Pseudoleskeella sibirica																				
[illegible]							1							1				1	1	1
Ptilidium californicum						1								1						
[illegible]																				
Pylaisiella polyantha														1				1		
[illegible]						1														
Racomitrium heterostichum																				
[illegible]																				
Racomitrium sudeticum																				
[illegible]																				
Rhizomnium magnifolium						1					1									
[illegible]											1									
Rhizomnium pseudopunctatum						1					1									
[illegible]																				
Rhytidiadelphus triquetrus																				
[illegible]										1										
Rhytidium rugosum																				
[illegible]				1		1				1	1									
Sanionia uncinata	1					1					1			1				1		
[illegible]																				
Schistidium apocarpum			1		1	1	1							1		1	1		1	
[illegible]		1	1		1	1	1													1
Schistidium tenerum																				
[illegible]						1														
Scouleria aquatica						1														
[illegible]																				
Seligeria campylopoda																				
[illegible]																				
Sphagnum angustifolium											1									
[illegible]																				
Sphagnum russowii											1									
[illegible]																				
Sphagnum teres											1									
[illegible]																		1		
Taylonia serrata																				
[illegible]																				
Tetraplodon angustatus																				

Species	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
[illegible]																				
Timmia austriaca				1		1														
[illegible]																				
Tomenthypnum nitens																				
[illegible]					1			1	1					1						1
Tortella inclinata																				
[illegible]			1		1		1	1						1				1		1
Tortula bartramii																				
[illegible]																				
Tortula mucronifolia														1				1		
[illegible]	1	1	1			1	1	1	1					1						1
Tortula papillosissima																1				
[illegible]			1		1	1	1		1		1	1	1	1	1	1	1	1	1	1
Tortula subulata																				
[illegible]																				
Warnstorfia pseudostramines						1														
[illegible]																				

Species	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
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Amblystegium juratzkanum																				
[illegible]																			1	
Amblystegium varium																				
[illegible]				1										1						1
Andreaea rupestris					1							1		1						
[illegible]																				
Atrichum selwynii																				
[illegible]																				
Aulacomnium palustre				1																
[illegible]																				
Barbula convoluta																				
[illegible]																				
Barbula unguiculata																				
[illegible]				1					1					1		1				1
Blindia acuta																				
[illegible]				1					1					1						1
Brachythecium asperrimum		1									1									
[illegible]	1																			
Brachythecium campestre																				
[illegible]				1	1	1	1		1					1		1				1
Brachythecium erythrorrhizon		1			1				1		1		1	1					1	1
[illegible]																				
Brachythecium frigidum		1									1									
[illegible]												1								
Brachythecium leibergii	1				1						1	1			1		1			
[illegible]											1									
Brachythecium nelsonii											1			1						
[illegible]	1				1			1		1	1	1	1	1	1		1	1	1	
Brachythecium plumosum																				
[illegible]	1					1		1						1					1	1
Brachythecium rivulare											1									
[illegible]																				
Brachythecium salebrosum		1							1		1									1
[illegible]						1														
Brachythecium velutinum				1	1		1					1		1	1					1
[illegible]						1	1									1				1
Bryum algovicum																1				
[illegible]																1				
Bryum caespiticium						1										1	1			
[illegible]		1		1																
Bryum capillare													1							1
[illegible]											1									
Bryum elegans					1															
[illegible]		1							1		1						1			
Bryum miniatum																				
[illegible]													1							
Bryum pallescens		1				1														
[illegible]		1	1						1		1									1
Bryum stirtonii									1				1							1
[illegible]		1												1						
Calliergon giganteum																				
[illegible]																				
Campylium chrysophyllum																				
[illegible]																				
Campylium hispidulum																				
[illegible]																				
Campylium radicale																				
[illegible]			1								1									1
Catascopium nigritum																				
[illegible]				1		1							1			1	1	1		
Cirriphyllum cirrosum																				1
[illegible]		1																		
Climacium dendroides																				
[illegible]																				
Coscinodon calyptratus																				
[illegible]			1	1																
Desmatodon latifolius				1					1				1	1		1		1		1
[illegible]																1				
Dichodontium olympicum																				
[illegible]											1									1
Dicranella schreberiana																				
[illegible]		1		1	1				1			1	1	1	1					1
Dicranum acutifolium																		1		
[illegible]									1											1
Dicranum brevifolium	1				1															
[illegible]																				
Dicranum fuscescens						1						1			1					
[illegible]					1															1
Dicranum pallidisetum					1													1		

Species	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Dicranum scoparium												1						1		
Dicranum undulatum												1								
Didymodon rigidulus																				
Distichium capillaceum		1					1													
Ditrichum flexicaule				1		1	1		1					1		1				1
Drepanocladus brevifolius						1	1		1											1
Dryptodon patens																				1
Encalypta ciliata												1								
Encalypta procera							1													
Encalypta spathulata						1	1													
Eurhynchium pulchellum				1		1	1		1					1						1
Fontinalis antipyretica																				
Grimmia affinis					1															
Grimmia anomala		1		1			1									1				
Grimmia dupretii				1		1			1				1			1				1
Grimmia montana		1		1	1										1					
Grimmia tenerrima				1	1								1							
Grimmia trichophylla																				1
Hamatocaulis vernicosus			1	1		1	1													1
Helodium blandowii																				
Heterocladium procurrens						1														
Homalothecium nevadense						1	1													
Hygrohypnum bestii		1									1									
Hygrohypnum molle																				1
Hylocomium splendens		1									1									
Hypnum cupressiforme					1				1											
Hypnum pallescens			1	1			1													
Hypnum recurvatum							1													
Hypnum vaucheri				1	1	1	1		1							1				1
Kiaeria starkei							1									1				
Leptodictyum humile	1			1									1	1						
Lescuraea saxicola											1									
Limprichtia revolvens					1		1		1					1						1
Mnium ambiguum																				
Mnium blyttii					1								1	1						1
Mnium spinulosum		1									1			1						1
Myurella julacea												1								
Orthothecium chryseum	1					1	1		1		1				1					
Orthotrichum alpestre																				1
Orthotrichum sudeticum					1		1													
Orthotrichum laevigatum						1														
					1	1	1													

Species	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Orthotrichum pallens																				
Orthotrichum pulchellum							1													
Orthotrichum speciosum																				
Paraleucobryum enerve			1																	1
Philonotis yezoana		1		1					1		1			1						1
Plagiomnium cuspidatum																				
Plagiomnium insigne											1									
Plagiopus oederiana																				
Plagiothecium denticulatum								1			1	1			1		1	1	1	
Platydictya jungermannioides	1				1							1						1		
Pogonatum urnigerum				1		1	1		1		1			1						1
Pohlia bolanderi				1					1				1							
Pohlia cruda				1														1		
Pohlia drummondii						1			1		1		1	1		1				1
Pohlia nutans	1				1			1		1		1	1		1		1	1		
Pohlia obtusifolia																				
Pohlia polymorpha											1									
Pohlia sphagnicola																				
Polytrichastrum alpinum		1									1								1	
Polytrichum juniperinum		1																		1
Polytrichum piliferum	1			1	1							1	1		1			1		
Pseudocalliergon turgescens				1					1				1		1			1		
Pseudoleskea incurvata																				1
Pseudoleskea patens	1					1			1	1							1		1	1
Pseudoleskea radicosa		1												1					1	
Pseudoleskeella sibirica	1	1		1	1			1	1	1		1	1	1	1		1	1	1	1
Pterigynandrum filiforme																			1	
Pylaisiella polyantha						1	1		1					1						1
Racomitrium heterostichum																				
Racomitrium sudeticum												1								
Rhizomnium gracile					1							1						1		
Rhizomnium magnifolium																				
Rhizomnium pseudopunctatum											1									
Rhytidiadelphus triquetrus											1									
Rhytidium rugosum																				
Sanionia uncinata	1											1								
Schistidium apocarpum	1	1			1			1			1			1	1			1	1	1
Schistidium tenerum						1	1		1					1		1				1
Scouleria aquatica		1		1					1											1
Seligeria campylopoda																				
Sphagnum angustifolium						1														1
Sphagnum fuscum						1														
Sphagnum russowii																				
Sphagnum teres																				
Sphagnum warnstorfii																				
Tayloria serrata																				
Tetraplodon pallidus																				
Tetraplodon angustatus																				

Species	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
[illegible]																				
Timmia austriaca					1	1	1		1		1			1						1
[illegible]						1														1
Tomenthypnum nitens																				
[illegible]				1			1									1				
Tortella inclinata																				
[illegible]				1		1	1													
Tortula bartramii																				
[illegible]																				
Tortula mucronifolia				1												1				
[illegible]		1		1	1	1			1				1	1						1
Tortula papillosissima																				
[illegible]				1	1	1	1		1				1	1		1				1
Tortula subulata																				
[illegible]																				
Warnstorfia pseudostramines																				
[illegible]				1																

Species	101	102	103	104	105	106	107	108	109	110	111	112	Freq
[illegible]													[illegible]
Amblystegium juratzkanum													10
[illegible]				[illegible]			[illegible]			[illegible]			[illegible]
Amblystegium varium													1
[illegible]			[illegible]									[illegible]	[illegible]
Andreaea rupestris	1												4
[illegible]												[illegible]	[illegible]
Atrichum selwynii													5
[illegible]							[illegible]						[illegible]
Aulacomnium palustre	1							1		1			21
[illegible]													[illegible]
Barbula convoluta													1
[illegible]													[illegible]
Barbula unguiculata													2
[illegible]												[illegible]	[illegible]
Blindia acuta			1										1
[illegible]			[illegible]				[illegible]			[illegible]		[illegible]	[illegible]
Brachythecium aspernmum	1	1											8
[illegible]			[illegible]										[illegible]
Brachythecium campestre													1
[illegible]				[illegible]	[illegible]		[illegible]	[illegible]		[illegible]			[illegible]
Brachythecium erythrorrhizon	1	1	1				1	1		1			38
[illegible]													1
Brachythecium frigidum	1	1											12
[illegible]								[illegible]		[illegible]			[illegible]
Brachythecium leibergii	1			1			1	1	1	1			36
[illegible]													[illegible]
Brachythecium nelsonii	1												13
[illegible]		[illegible]					[illegible]	[illegible]	[illegible]	[illegible]			[illegible]
Brachythecium plumosum													1
[illegible]							[illegible]	[illegible]	[illegible]	[illegible]			[illegible]
Brachythecium rivulare	1	1											12
[illegible]												[illegible]	[illegible]
Brachythecium salebrosum				1			1	1		1		1	44
[illegible]													[illegible]
Brachythecium velutinum						1	1			1			33
[illegible]				[illegible]		[illegible]	[illegible]			[illegible]			[illegible]
Bryum algovicum													1
[illegible]													[illegible]
Bryum caespiticium			1	1			1			1			23
[illegible]												[illegible]	[illegible]
Bryum capillare						1	1			1			24
[illegible]													[illegible]
Bryum elegans													2
[illegible]				[illegible]				[illegible]		[illegible]			[illegible]
Bryum miniatum													2
[illegible]													[illegible]
Bryum pallescens										1		1	9
[illegible]	[illegible]	[illegible]	[illegible]										[illegible]
Bryum stirtonii													8
[illegible]	[illegible]												[illegible]
Calliergon giganteum													1
[illegible]													[illegible]
Campylium chrysophyllum												1	9
[illegible]													[illegible]
Campylium hispidulum													4
[illegible]													[illegible]
Campylium radicale													1
[illegible]		[illegible]	[illegible]										[illegible]
Catascopium nigritum													1
[illegible]			[illegible]		[illegible]		[illegible]		[illegible]				[illegible]
Cirriphyllum cirrosum	1												2
[illegible]													[illegible]
Climacium dendroides													2
[illegible]													[illegible]
Coscinodon calyptratus													1
[illegible]	[illegible]	[illegible]	[illegible]										[illegible]
Desmatodon latifolius	1	1		1			1	1		1			25
[illegible]													[illegible]
Dichodontium olympicum		1											1
[illegible]	[illegible]	[illegible]	[illegible]										[illegible]
Dicranella schrebenana													1
[illegible]	[illegible]							[illegible]		[illegible]			[illegible]
Dicranum acutifolium													1
[illegible]													[illegible]
Dicranum brevifolium													5
[illegible]													[illegible]
Dicranum fuscescens								1					12
[illegible]													[illegible]
Dicranum pallidisetum													3

Species	101	102	103	104	105	106	107	108	109	110	111	112	Freq
[illegible]													4
Dicranum scoparium							1	1				1	31
[illegible]													4
Dicranum undulatum													1
[illegible]													1
Didymodon rigidulus													4
[illegible]	1					1							14
Distichium capillaceum			1	1		1						1	27
[illegible]													1
Ditrichum flexicaule			1				1					1	32
[illegible]													12
Drepanocladus brevifolius													1
[illegible]													1
Dryptodon patens													4
[illegible]													8
Encalypta ciliata												1	7
[illegible]													8
Encalypta procera						1							12
[illegible]												1	14
Encalypta spathulata													3
[illegible]													12
Eurhynchium pulchellum			1	1			1			1		1	41
[illegible]				1									9
Fontinalis antipyretica													1
[illegible]													1
Grimmia affinis													1
[illegible]						1							11
Grimmia anomala	1	1											6
[illegible]				1								1	5
Grimmia dupretii					1		1	1					34
[illegible]												1	1
Grimmia montana		1		1								1	16
[illegible]													1
Grimmia tenerrima												1	11
[illegible]												1	8
Grimmia trichophylla													1
[illegible]			1										10
Hamatocaulis vernicosus													3
[illegible]													1
Helodium blandowii													3
[illegible]													1
Heterocladium procurrens													2
[illegible]						1						1	20
Homalothecium nevadense												1	6
[illegible]						1							5
Hygrohypnum bestii	1	1											7
[illegible]	1		1										10
Hygrohypnum molle	1	1											3
[illegible]	1	1											8
Hylocomium splendens												1	14
[illegible]													8
Hypnum cupressiforme						1							8
[illegible]													4
Hypnum pallescens													4
[illegible]													1
Hypnum recurvatum													1
[illegible]						1	1					1	34
Hypnum vaucheri						1							13
[illegible]						1						1	11
Kiaeria starkei		1											3
[illegible]	1												13
Leptodictyum humile													2
[illegible]													4
Lescuraea saxicola													5
[illegible]												1	13
Limprichtia revolvens			1									1	8
[illegible]													2
Mnium ambiguum	1												8
[illegible]						1							14
Mnium blyttii	1												10
[illegible]													4
Mnium spinulosum							1	1	1	1			26
[illegible]				1		1						1	17
Myurella julacea												1	6
[illegible]							1	1					24
Orthothecium chryseum													2
[illegible]							1						6
Orthotrichum alpestre						1				1		1	15
[illegible]										1			7
Orthotrichum laevigatum												1	21

Species	101	102	103	104	105	106	107	108	109	110	111	112	Freq
[illegible]							1						3
Orthotrichum pallens						1							6
[illegible]						1							8
Orthotrichum pulchellum													1
[illegible]						1							4
Orthotrichum speciosum							1						8
[illegible]													3
Paraleucobryum enerve													2
[illegible]	1	1	1										24
Philonotis yezoana												1	1
[illegible]													1
Plagiomnium cuspidatum													5
[illegible]													3
Plagiomnium insigne								1					2
[illegible]								1					11
Plagiopus oederiana													2
[illegible]													1
Plagiothecium denticulatum				1			1	1					18
[illegible]			1					1					21
Platydictya jungermannioides				1		1							33
[illegible]							1						20
Pogonatum urnigerum		1											6
[illegible]													1
Pohlia bolanderi	1		1										12
[illegible]	1		1	1								1	30
Pohlia drummondii	1	1											8
[illegible]	1						1	1		1			25
Pohlia obtusifolia													1
[illegible]													2
Pohlia sphagnicola													4
[illegible]	1	1											15
Polytrichastrum alpinum	1											1	9
[illegible]													3
Polytrichum juniperinum	1						1	1					27
[illegible]													31
Polytrichum piliferum													13
[illegible]													1
Pseudocalliergon turgescens													1
[illegible]													7
Pseudoleskea incurvata		1		1	1		1						26
[illegible]	1	1					1			1	1	1	17
Pseudoleskea radicosa	1	1	1	1	1	1	1	1	1	1	1	1	65
[illegible]											1		8
Pseudoleskeella sibirica													1
[illegible]						1	1					1	20
Ptergynandrum filiforme													6
[illegible]							1			1			12
Pylaisella polyantha							1						15
[illegible]													8
Racomitrium heterostichum	1												6
[illegible]												1	1
Racomitrium sudeticum	1	1											5
[illegible]													1
Rhizomnium magnifolium	1												8
[illegible]													4
Rhizomnium pseudopunctatum													5
[illegible]													2
Rhytidiadelphus triquetrus													5
[illegible]							1			1			16
Rhytidium rugosum													1
[illegible]	1						1	1					22
Sanionia uncinata	1		1				1	1		1		1	49
[illegible]													1
Schistidium apocarpum			1			1				1		1	36
[illegible]	1	1	1									1	24
Schistidium tenerum													1
[illegible]													3
Scouleria aquatica													1
[illegible]													1
Seligeria campylopoda													3
[illegible]													1
Sphagnum angustifolium													2
[illegible]													1
Sphagnum russowii													5
[illegible]													1
Sphagnum teres													3
[illegible]													5
Taylonia serrata								1					1
[illegible]													3
Tetraplodon angustatus													1

Species	101	102	103	104	105	106	107	108	109	110	111	112	Freq
[illegible]													1
Timmia austriaca	1						1						30
[illegible]													4
Tomenthypnum nitens													5
[illegible]			1								1		18
Tortella inclinata													2
[illegible]			1	1		1	1			1	1		17
Tortula bartramii													2
[illegible]													1
Tortula mucronifolia						1	1						19
[illegible]	1	1		1			1			1			24
Tortula papillosissima													1
[illegible]				1	1	1	1			1	1		64
Tortula subulata													2
[illegible]													1
Warnstorfia pseudostraminea													2
[illegible]				1	1								8

Appendix C. Environmental data for 112 sites sampled in Waterton Lakes National Park in Summer, 1997. Site types are explained in table 3.1. Codes for environmental data correspond to those in table 3.2. UTM northing and easting were used to derive LATITUDE and LONGITUDE respectively.

Site No.	Site Type	UTM	Northing	Easting	Aspect1	Aspect2	Aspect3	Slope	Elevation	Moisture	Water	Soil	Mineral	Organic
2	Talus	11	712180	5449351				29	2022	1.00	0.00	5.00	4.00	1.00
4	Deciduous forest	12	283650	5442417				6	1412	3.00	0.00	95.00	1.00	94.00
6	Deciduous forest	12	285198	5443061				13	1406	2.50	0.00	75.00	0.00	75.00
8	Deciduous forest	12	297861	5438264				9	1600	2.00	0.00	95.00	0.00	95.00
10	Deciduous forest	12	303881	5433702				3	1452	2.00	0.00	85.00	0.00	85.00
12	Grassland	11	715489	5445197				27	1590	1.00	0.00	100.00	75.00	25.00
14	Coniferous forest	12	285566	5438585				21	1516	2.00	0.00	90.00	0.00	100.00
16	Forested cliff	12	287166	5437868	188294.8	146947.2	195830.5	41	1501	2.00	0.00	30.00	1.00	30.00
18	Wetland	12	299935	5437269				0	1562	4.00	1.00	95.00	0.00	100.00
20	Coniferous forest	12	300046	5437079				10	1562	4.00	0.00	100.00	0.00	100.00
22	Wetland	12	289337	5441557				0	1365	5.00	30.00	70.00	1.00	69.00
24	Stream	12	286694	5435971	18084.8	42642.36	1519.22	50	1338	5.00	10.00	25.00	20.00	5.00
26	Deciduous forest	12	293581	5442393				0	1323	4.00	35.00	65.00	1.00	64.00
28	Wetland	12	292825	5441634				0	1329	5.00	95.00	1.00	0.00	1.00
30	Alluvial gravel	12	293150	5439355				0	1353	2.00	0.00	30.00	30.00	0.00
32	Coniferous forest	12	287015	5437422				32	1408	3.00	0.00	70.00	10.00	60.00
34	Talus	12	288404	5442950				30	1561	1.00	0.00	90.00	89.00	1.00
36	Stream	12	288351	5444000	80919.1	1837.28	17096.24	45	1694	4.00	0.00	1.00	0.50	0.50
38	Mixedwood forest	12	287251	5432813				0	1367	0.00	0.00	100.00	0.00	100.00
40	Forested cliff	12	287200	5433100	2582.96	77504.82	15195.15	75	1357	2.00	0.00	1.00	0.10	0.90
42	Alluvial gravel	11	715604	5447228				0	1566	1.50	0.00	85.00	85.00	0.00
44	Stream	11	716590	5446351	181915.2	42642.36	117364.8	10	1573	3.00	0.00	40.00	32.00	8.00
46	Wetland	11	715286	5434529				0	1768	5.00	50.00	50.00	0.00	50.00
48	Coniferous forest	11	715985	5434186				24	1735	2.50	0.00	100.00	20.00	80.00
50	Alluvial gravel	12	303963	5435053				0	1363	1.00	0.00	40.00	40.00	0.00
52	Stream	11	712221	5449491	67443.18	194551.9	143837.1	1	1990	5.00	5.00	95.00	57.00	38.00
54	Talus	11	712858	5449138				33	1879	2.00	0.00	1.00	0.80	0.20
56	Unforested cliff	11	718313	5438193	1837.28	119080.9	44080.71	37	1635	2.50	0.00	55.00	90.00	10.00
58	Stream	11	715938	5434557	96510.05	60.92	26864.63	15	1680	5.00	0.00	25.00	70.00	30.00
60	Wetland		292377	5443602				0	1282	5.00	20.00	100.00	0.00	100.00
62	Meadow	11	714458	5437489				3	2022	2.00	0.00	100.00	80.00	20.00
64	Coniferous forest	11	715815	5438022				22	1950	2.00	0.00	95.00	0.00	95.00
66	Stream	11	718098	5438123	84356.55	1231.17	19098.3	3	1635	4.00	0.00	15.00	12.00	3.00
68	Unforested cliff	11	716688	5438248	98254.76	15.23	28066.02	82	1861	1.00	0.00	1.00	1.00	0.00
70	Coniferous forest	11	717223	5438171				20	1747	2.50	0.00	85.00	5.00	80.00
72	Grassland	12	284247	5443304				22	1505	2.00	0.00	100.00	80.00	20.00
74	Coniferous forest	12	296209	5438383				15	1631	2.00	0.00	100.00	50.00	50.00
76	Grassland	12	286682	5448015				27	1644	1.00	0.00	100.00	70.00	30.00

Site No.	Site Type	UTM	Northing	Easting	Aspect1	Aspect2	Aspect3	Slope	Elevation	Moisture	Water	Soil	Mineral	Organic
76	Deciduous forest	12	287366	5446547				28	1534	3.00	0.00	100.00	20.00	80.00
80	Talus	12	282760	5434819				22	1864	1.00	0.00	1.00	1.00	0.00
82	Stream	12	283019	5435530	98254.76	199984.8	169465.9	10	1828	5.00	20.00	30.00	18.00	12.00
84	Unforested cliff	11	711902	5449587	74118.1	3407.42	13397.46	78	2012	2.00	0.00	5.00	4.50	0.50
86	Unforested cliff	12	281771	5439549	29289.32	29289.32	0	72	1608	2.00	0.00	15.00	13.50	1.50
88	Alder	11	708310	5447313				42	1912	3.00	0.00	100.00	20.00	80.00
90	Meadow	11	708042	5447360				32	1962	2.00	0.00	50.00	20.00	30.00
92	Coniferous forest	11	709758	5447420				10	1736	3.00	0.00	80.00	12.00	68.00
94	Unforested cliff	11	707591	5445760	47008.07	184804.8	122495.1	90	1738	2.00	0.00	5.00	2.50	2.50
96	Talus	12	280704	5433845				30	2284	1.00	0.00	1.00	0.40	0.60
98	Coniferous forest	11	718202	5433515				20	2086	2.00	0.00	95.00	45.00	40.00
100	Unforested cliff	11	714458	5437489	22285.4	162932	89547.15	75	2005	2.00	0.00	20.00	7.00	13.00
102	Stream	12	292534	5431255	168199.8	173135.4	199939.1	18	1982	5.00	37.50	50.00	10.00	40.00
104	Coniferous scrub	12	292147	5432464				35	1874	1.00	0.00	30.00	25.00	5.00
106	Forested cliff	12	289423	5433957	199863	105233.6	174314.5	90	1552	2.00	0.00	5.00	4.50	0.50
108	Coniferous scrub	11	710296	5444103				15	1730	2.00	0.00	100.00	10.00	90.00
110	Mixedwood forest	11	713653	5443944				18	1612	2.00	0.00	100.00	30.00	70.00
112	Forested cliff	12	285273	5434346	60926.89	7949.51	7281.61	78	1809	1.00	0.00	1.00	0.50	0.50

Site No.	Site Type	Expsoil	Soiltex	Rock	Exprock	Rough	Microtop	Stability	Deciduos	Conifer	Treehite	Wood	Shrubs	Herbs
2	Talus	1.00	3.00	95.00				3.50	0.00	0.00		1.00	0.00	1.00
4	Deciduous forest	0.00	2.00	0.00				5.00	75.00	0.00	16.50	5.00	95.00	80.00
6	Deciduous forest	0.00	2.00	0.00				5.00	95.00	0.00	7.60	25.00	30.00	70.00
8	Deciduous forest	0.00	3.00	0.00				5.00	60.00	0.00	3.70	5.00	1.00	95.00
10	Deciduous forest	1.00	3.00	0.00				5.00	75.00	0.00	7.10	15.00	10.00	90.00
12	Grassland	1.00	2.00	1.00				2.00	0.00	0.00		1.00	10.00	100.00
14	Coniferous forest	1.00	2.00	7.50				4.00	0.00	80.00	18.50	45.00	75.00	60.00
16	Forested cliff	1.00	2.00	90.00	80.00	3.00	3.00	3.00	0.00	60.00		1.00	20.00	40.00
18	Wetland	1.00	2.00	0.00				5.00	0.00	1.00		1.00	70.00	50.00
20	Coniferous forest	0.00	2.00	0.00				5.00	0.00	65.00		1.00	10.00	50.00
22	Wetland	1.00	3.00	0.00				5.00	70.00	0.00		1.00	65.00	90.00
24	Stream	1.00	1.00	65.00	60.00	3.00	4.00	3.00	10.00	1.00		5.00	20.00	20.00
26	Deciduous forest	1.00	1.00	1.00				5.00	50.00	0.00	7.10	5.00	15.00	75.00
28	Wetland	1.00	1.00	0.00				5.00	0.00	0.00		1.00	1.00	90.00
30	Alluvial gravel	15.00	2.00	70.00				2.00	0.00	0.00		1.00	30.00	40.00
32	Coniferous forest	0.00	1.00	1.00				3.00	1.00	50.00	17.10	30.00	30.00	30.00
34	Talus	1.00	1.00	5.00				1.00	0.00	0.00		1.00	10.00	15.00
36	Stream	1.00	1.00	95.00	90.00	2.00	3.00	1.00	0.00	0.00		1.00	0.00	1.00
38	Mixedwood forest	0.00	2.00	0.00				5.00	40.00	40.00	12.80	5.00	10.00	60.00
40	Forested cliff	0.00	1.00	95.00	50.00	3.00	4.00	4.00	0.00	5.00		1.00	50.00	1.00
42	Alluvial gravel	1.00	1.00	15.00				2.00	1.00	1.00		1.00	10.00	90.00
44	Stream	0.00	2.00	60.00	35.00	1.00	4.00	4.00	0.00	0.00		0.00	1.00	30.00
46	Wetland	0.00	2.00	0.00				5.00	0.00	20.00		5.00	40.00	15.00
48	Coniferous forest	1.00	2.00	0.00				5.00	0.00	45.00	18.90	5.00	70.00	65.00
50	Alluvial gravel	35.00	3.00	60.00				2.00	5.00	1.00		1.00	10.00	30.00
52	Stream	1.00	2.00	1.00	1.00	2.00	3.00	4.00	1.00	25.00		5.00	1.00	20.00
54	Talus	1.00	2.00	95.00				2.00	0.00	0.00		1.00	15.00	5.00
56	Unforested cliff	1.00	1.00	45.00	30.00	3.00	4.00	3.00	0.00	5.00		1.00	15.00	40.00
58	Stream	1.00	2.00	75.00	50.00	2.00	4.00	4.00	0.00	20.00		1.00	65.00	1.00
60	Wetland	1.00	3.00	0.00				5.00	1.00	0.00		15.00	85.00	85.00
62	Meadow	1.00	2.00	1.00				5.00	0.00	0.00		1.00	1.00	95.00
64	Coniferous forest	1.00	2.00	1.00				5.00	0.00	50.00	6.80	5.00	35.00	80.00
66	Stream	1.00	1.00	85.00	80.00	2.00	3.50	4.00	1.00	50.00		5.00	40.00	5.00
68	Unforested cliff	1.00	3.00	99.00	99.00	2.00	4.00	4.00	0.00	0.00		0.00	1.00	1.00
70	Coniferous forest	1.00	2.00	1.00				5.00	0.00	60.00	16.50	15.00	5.00	75.00
72	Grassland	1.00	2.50	1.00				5.00	0.00	15.00		1.00	30.00	60.00
74	Coniferous forest	1.00	3.00	1.00				5.00	0.00	40.00	9.20	5.00	10.00	70.00
76	Grassland	1.00	3.00	1.00				5.00	0.00	5.00		1.00	10.00	95.00

Site No.	Site Type	Expsoil	Soiltex	Rock	Exprock	Rough	Microtop	Stability	Deciduos	Conifer	Treehite	Wood	Shrubs	Herbs
78	Deciduous forest	1.00	2.00	0.00				5.00	50.00	0.00	9.60	1.00	10.00	95.00
80	Talus	1.00	0.00	99.00				2.00	0.00	0.00		0.00	1.00	1.00
82	Stream	1.00	2.00	70.00	65.00	3.00	3.00	3.00	0.00	1.00		10.00	15.00	20.00
84	Unforested cliff	1.00	2.50	95.00	90.00	2.00	4.00	4.00	0.00	5.00		0.50	1.00	1.00
86	Unforested cliff	1.00	3.00	85.00	80.00	2.00	4.00	4.00	5.00	5.00		1.00	5.00	10.00
88	Alder	1.00	2.00	0.00				1.00	0.00	0.00		1.00	95.00	90.00
90	Meadow	0.00	2.00	50.00				2.00	0.00	1.00		1.00	0.00	95.00
92	Coniferous forest	1.00	2.00	5.00				5.00	0.00	45.00	6.70	10.00	80.00	40.00
94	Unforested cliff	1.00	2.00	95.00	85.00	2.00	4.00	4.00	1.00	5.00		1.00	5.00	5.00
96	Talus	1.00	3.00	99.00				1.00	0.00	0.00		0.00	0.00	5.00
98	Coniferous forest	1.00	2.00	1.00				5.00	0.00	35.00	6.60	1.00	40.00	80.00
100	Unforested cliff	1.00	2.00	80.00	76.00	3.00	4.00	4.00	0.00	15.00		1.00	5.00	5.00
102	Stream	0.00	2.00	50.00	40.00	2.00	2.00	4.50	0.00	5.00		1.00	1.00	30.00
104	Coniferous scrub	1.00	2.50	70.00				1.50	0.00	91.00		5.00	10.00	30.00
106	Forested cliff	1.00	3.00	95.00	95.00	2.00	4.00	5.00	0.00	50.00		1.00	20.00	1.00
108	Coniferous scrub	1.00	2.00	0.00				5.00	0.00	91.00		1.00	1.00	60.00
110	Mixedwood forest	1.00	2.00	1.00				5.00	50.00	50.00	8.90	1.00	40.00	80.00
112	Forested cliff	1.00	3.00	99.00	95.00	2.00	3.00	4.00	0.00	1.00		0.00	0.00	1.00

Site No.	Site Type	Bryos	Litter	complexity
2	Talus	5.00	0.00	9.00
4	Deciduous forest	1.00	5.50	6.00
6	Deciduous forest	1.00	11.50	5.00
8	Deciduous forest	1.00	3.00	5.00
10	Deciduous forest	1.00	2.50	5.00
12	Grassland	10.00	1.00	6.00
14	Coniferous forest	5.00	4.00	11.00
15	Stream	5.00	1.00	15.00
16	Forested cliff	5.00	4.00	14.00
18	Wetland	50.00	0.50	6.00
20	Coniferous forest	80.00	2.00	7.00
22	Wetland	1.00	2.00	8.00
24	Stream	7.50	5.00	14.00
26	Deciduous forest	60.00	1.50	9.00
28	Wetland	1.00	1.00	4.00
30	Alluvial gravel	1.00	0.00	11.00
32	Coniferous forest	85.00	4.00	11.00
34	Talus	1.00	0.00	8.00
36	Stream	1.00	0.50	11.00
38	Mixedwood forest	1.00	3.50	7.00
40	Forested cliff	50.00	0.00	12.00
42	Alluvial gravel	1.00	4.00	10.00
44	Stream	25.00	0.50	10.00
46	Wetland	50.00	0.50	7.00
48	Coniferous forest	50.00	3.00	6.00
50	Alluvial gravel	1.00	0.50	7.00
52	Stream	80.00	0.50	11.00
54	Talus	1.00	2.00	8.00
55	Coniferous forest	75.00	3.00	4.00
56	Unforested cliff	40.00	2.00	11.00
58	Stream	40.00	1.50	13.00
60	Wetland	35.00	1.00	7.00
62	Meadow	1.00	0.50	6.00
64	Coniferous forest	15.00	1.00	8.00
66	Stream	20.00	2.00	15.00
68	Unforested cliff	1.00	0.50	10.00
70	Coniferous forest	5.00	2.80	5.00
72	Grassland	1.00	0.50	7.00
74	Coniferous forest	1.00	1.50	7.00
76	Grassland	1.00	1.00	5.00

Site No.	Site Type	Bryos	Litter	Complexity
78	Deciduous forest	1.00	2.80	6.00
80	Talus	1.00	0.50	7.00
82	Stream	35.00	0.50	14.00
84	Unforested cliff	10.00	0.50	14.00
86	Unforested cliff	5.00	1.50	11.00
88	Alder	10.00	1.00	5.00
90	Meadow	80.00	0.50	6.00
92	Coniferous forest	50.00	3.00	11.00
94	Unforested cliff	15.00	0.00	15.00
96	Talus	1.00	0.00	4.00
98	Coniferous forest	5.00	1.20	10.00
100	Unforested cliff	5.00	2.00	13.00
102	Stream	45.00	0.00	15.00
104	Coniferous scrub	1.00	1.50	11.00
106	Forested cliff	1.00	0.50	10.00
108	Coniferous scrub	1.00	3.00	6.00
110	Mixedwood forest	10.00	1.50	10.00
112	Forested cliff	5.00	0.50	10.00